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ON THE LEAF AND SPOROCARP OF PILULARIA.

DUNCAN S. JOHNSON.

(WITH PLATES I–III)

DURING the course of some work on the development of the foliar structures of *Marsilia quadrifolia* L., the results of which have been published elsewhere ('98), a brief examination was also made of the same structures in the related Pilularia. Certain features observed here suggested the desirability of making a more careful study of the latter genus, and following out in detail all stages of the development for comparison with the same stages in Marsilia.

Through the kindness of Professor Eugenius Warming, Dr. Ostenfeld Hansen, of Copenhagen, collected for me in July 1897 a considerable quantity of fruiting material of *Pilularia globulifera* L. With this material the work embodied in the present paper has been prosecuted at the biological laboratory of the Johns Hopkins University, while holding the Adam T. Bruce fellowship for 1897–8.

The material was fixed in 95 per cent. alcohol, which seemed to give very good results except in the older stages, where the preparation of certain tissues of the capsule for the gelatinization, which causes the bursting of the capsule, had already begun. In this stage the sporocarps were often considerably shrunken, as happens in Marsilia after using other fixing agents unless great care is used in running up through the alcohols.

Sections of the structures studied were cut in paraffine, stained rather lightly in Mayer's haemalum, and then strongly with Bismarck brown in saturated solution in 70 per cent. alcohol.

THE LEAF.

The leaves of Pilularia arise, in acropetal succession, on the right and left sides alternately of the upper surface of the stem. Each leaf originates in a large cell from which a typical two-sided apical cell is cut out by curved anticlines. The apical cell thus formed has its longer axis directed toward the stem apex (*L*, *fig. 1*), as was shown by Bower ('84).

This apical cell swells out beyond the general surface of the stem and cuts off segments, alternately toward the right and left of the latter and of the leaf itself. The number of segments formed is probably about fifteen pairs. In several young leaves where the segments could be counted the number was found to be ten or eleven on each side of the apical cell, but in older leaves where the segments could not be satisfactorily counted the number was apparently considerably greater, at least as many as fifteen.

By the growth and division of these segments a papilla-like organ is formed, which soon begins to curve in ventrally (*L*, *fig. 3*) toward and above the stem apex. This circinate coiling continues with growth of the leaf until, when a centimeter long, the tip may form a flat spiral of two turns or more, of which the inner projects out laterally beyond the plane of the outer, so that median sagittal sections cannot be obtained through the whole length of the leaf.

Up to quite a late period the apical cell can be distinguished, but whether its fate is finally like that to be described for the apical cell of the sporocarp was not determined. The shape of this is never three-sided, as described by Campbell ('93) in *P. Americana*, but is two-sided as stated by Meunier ('87), though the segments are not cut off toward the dorsal and ventral sides of the leaf as seems to be indicated in Meunier's figures, but to the right and left alternately as we have seen.

The primary division of the semicircular segments or "primary marginal cells" is quite regular and at first resembles exactly that described by Poirault ('90) and myself for Marsilia. The first wall formed is a longitudinal and radial anticline (*I, figs. 3, 4*) cutting off about one-third of the segment toward the dorsal side to form what we may call a section. The second is a similar wall (*II, figs. 2–4*) forming a second section next to the median wall of the leaf (or inner border of the segment), and leaving a "tertiary marginal cell" (*m* c^3, *fig. 4*). Then a transverse anticline (*t* a^1, *figs. 2, 3*) divides this marginal cell into two, an upper and a lower one. In each of these tertiary marginal cells a third longitudinal anticline appears (*III, figs. 3, 5*) nearly parallel to wall I. At this point the similarity to Marsilia ceases, for instead of forming two more sections, as in that plant, each marginal cell of the fourth grade is here divided by a pericline (*d w, fig. 6*), thus ending its function as a marginal cell.

The four primary divisions formed in each segment (leaving out of account the transverse anticlines which do not appear in a cross section of the leaf) develop in a way very like that found in the six primary divisions in the segments of the leaf of Marsilia. Section I very early cuts off by a pericline near the inner end (*p l w, fig. 4*) a cell which is to function as procambium. The outer end of the section is soon cut in halves by a longitudinal anticline (*h a, fig. 4*). Then sections II and III and the marginal cell form procambium at their inner ends (*p l w, fig. 6*), while at the outer ends of all the sections periclines, corresponding to that in the marginal cell, separate the protoderm and ground meristem layers which encircle the procambium (*figs. 6, 7*). No second portion of procambium is ever formed in section I, as happens in Marsilia.

The protoderm layer soon divides by periclines into epidermis and hypodermis (*e p* and *h y, figs. 7–9*) and the cells of these then divide by anticlines to form many cells, but each layer remains of a single cell in thickness even at maturity, as no more periclines are ever formed. The procambium throughout breaks up by numerous longitudinal walls and fewer transverse ones to

form the elongated cells of the axial vascular bundle (*a b*, *figs. 6–9*). Of the cells arising thus, one of the four first formed in the procambium of section II (*t r*, *figs. 6–9*) develops without further division by longitudinal walls into the large trachea of each side of the bundle. Whether transverse anticlines are formed in this in its later development could not be made out with certainty, but it agrees apparently with the trachea of the same bundle in Marsilia in remaining the full length of the segment. As the bundle progresses in its development the outer layer of the cells formed from the procambium becomes specialized as an endodermis or bundle sheath (*b s*, *figs. 8, 9*). The fact that the first wall formed in the procambium of section I does not correspond exactly with the halving anticline in the outer end of this section (*fig. 5*) makes it easy to distinguish procambium and ground meristem at this point (*figs. 6–8*). The leaf of Pilularia thus forms an exception to the general rule holding in the ferns, that the endodermis is formed from the ground meristem surrounding the bundle (Haberlandt, **'96,** p. 336); and agrees rather with the Juncaceæ and Cyperaceæ which have been studied by Haberlandt. I am inclined also to believe that Marsilia agrees with Pilularia in this respect, though it was not possible to determine this with absolute certainty as in the present case.

We may now turn to follow briefly the development of the ground meristem layer The two primary cells of this layer in section I and the single cell of each of the other three main divisions of the segment divide by a single pericline in each. The inner layer of cells thus formed, ten in number, constitutes the mesophyll layer (*m p*, *figs. 7–9*), which remains of this number (as seen in cross section) until maturity, being one cell thick and having no tannin sacs like those of Marsilia. Of the ten outer cells (*p c*, *figs. 7–9*), of which there are at this time several in the length of a segment, each gives rise to its part of one of the ten longitudinal partitions which separate the ten longitudinal air canals (*a c*, *figs. 7, 9*), in the leaf of Pilularia (Bischoff, **'28**). These air canals arise very early as small

intercellular spaces between the cells of the ground meristem and those of the hypodermis (*a c*, *figs. 7–9*) on the line of the median wall, of each section wall, and on the halving anticline of section I. The primary partition cells divide by periclines and thus increase in a radial direction as the leaf increases in diameter. At certain points the tips of these cells remain in contact with those of their fellows in adjoining sections laterally (as at the median wall and halving anticline in *fig. 8*). When viewed in tangential section (*pc*, *fig. 10*) it is seen that each cell of the partition elongates tangentially and forms thus a protuberance at the upper end on one side and at the lower end of the cell on the other side. Then when the next transverse anticline is formed it is slightly oblique and forms two wedge-like cells, each with a protuberance on one end and none at the other (*fig. 10*). These cells soon elongate with the growth in length of the leaf, and cells are cut off from each which are not in contact with their fellows laterally (*fig. 11*). Thus arise the longitudinal partitions which separate laterally the adjacent air canals. The protruding ends of the partition cells, which separate the divisions, at first short, of the same longitudinal canal from each other, are finally cut off by oblique anticlines (*c p*, *fig 11*) and form thus transverse partitions two cells broad from one longitudinal partition to the next. These cells do not divide further, as in Marsilia to form transverse partitions many cells in width, but elongate very greatly as the longitudinal partitions separate by the growth in circumference of the leaf. The latter, however, are closer together at the point where joined by the transverse partitions, and thus each longitudinal partition, as seen in tangential section, has a zigzag course from the base to the apex of the leaf. Both kinds of partitions remain one cell in thickness throughout, and both are perforated by pores, the "meats" of Meunier, which allow the free circulation of the enclosed air to all parts of the leaf.

The stomata which are present on both the leaf and the sporocarp and the peculiar trichomes which cover all the younger parts (Mettenius '**46**) have been carefully studied and figured

by Meunier, and for the sake of simplicity have been omitted from nearly all drawings in the present paper. We may note, however, that the origin of the trichome from a portion cut from the acroscopic end of an epidermal cell is practically the same as in Marsilia, though the regularity is not so striking.

As is well known (Bischoff '28), the mature leaf of Pilularia has no lamina whatever. We may consider it as quite probable, however, that the immediate ancestors of Pilularia and Marsilia had leaves possessing a lamina, which still persists in the latter genus, and we might expect to find some remnant or trace of this in Pilularia in the mode of division of the segments if not in the outward form. Keeping in mind then the mode of development of the lamina in Marsilia, by the continued activity of the marginal cells near the apex of the leaf, many segments in this region of the leaf of Pilularia were examined in search of any irregularity in the formation of cell walls, or of continued activity of the marginal cells. The results were always negative, and we must therefore conclude that the development of the leaf of Pilularia gives no indication that it has ever possessed a lamina.

THE SPOROCARP.

The sporocarp of Pilularia was considered by Hofmeister ('62) as a modified branch arising as an accessory bud at the base of the leaf. Alexander Braun ('70) and his pupil Russow ('72) dissent from this view, and on theoretical grounds consider it a segment or branch of the leaf; while Juranyi ('80) and Goebel ('82) confirm this latter view as a result of the study of the development of the sporocarp and the relation of its tissues to those of the neighboring leaf. Meunier ('87), however, while holding that the latter view is probably the correct one, thinks the evidence adduced is at fault, as the vascular bundle of the sporocarp, according to his observations, does not fuse first with that of the leaf, but with that of the stem itself. He then points out that the best evidence for this view will be the proof that both arise from the single apical cell of a foliar structure at first

unbranched. This he was not fortunate enough to obtain, and it was left for Campbell (**'93**) to show that this was the case in *P. Americana*, where he found the sporocarp arose from a single cell at the base of the leaf. In the development of the capsule of the sporocarp in Pilularia, Juranyi thought the soral cavities arose by a splitting of the internal tissues of the young capsule, as Russow had described for Marsilia. Goebel on the contrary held that these cavities were external in origin, and this view was later confirmed by the work of Meunier and Campbell.

According to Meunier's work the young sporocarp is developed from a two-sided (possibly a three-sided) apical cell which soon ceases to function as such, and growth is continued by the activity of four cells occupying the four corners of the tip of the sporocarp. Each of these cells was supposed to give rise to one of the four valves of the mature capsule with its sorus.

Meunier's figures of the vascular bundle system of the capsule and of the stalk show that the sporocarp is bilaterally symmetrical, and that the plane of symmetry separates the sori into a right pair and a left pair and does not pass through the middle of diagonally opposite sori as do the longitudinal sections figured by Meunier.

The latest work on the development of the capsule (Campbell **'93** and **'95**) indicates that one of the valves or lobes of the young capsule is developed directly from the apical cell of the sporocarp, being thus terminal in position, while a second appears lower down on the median line of the side toward the leaf, and the third and fourth on the right and left of this line respectively. This of course means that the plane of symmetry must pass through the upper and lower sori and between the other two, which does not agree well with the structure of the mature capsule of Pilularia as given by Meunier, or with the mode of development that I found in Marsilia. It was this difficulty in seeing how the structure of the mature capsule as given by Meunier could be developed in the manner described by Campbell that led me to take up the present work.

According to my own observations the sporocarp of Pilularia

arises on the inner and anterior side of the leaf, just above the axillary bud which is always present. As in Marsilia, a fertile branch of the stem has a sporocarp on nearly every leaf, but there is never more than one on the same leaf in Pilularia, or could any rudiment of a second be found.

The young sporocarp owes its origin to the formation of a two-sided apical cell in one of the marginal cells of the fourth grade in (probably) the first segment of the anterior side of the leaf (*F*, *fig. 12*). The difficulties of orientation were such that transverse sections of the leaf in this region were not frequently obtained, and it cannot be definitely stated therefore that the sporocarp arises in the quaternary marginal cell, rather than the tertiary one, but the evidence obtained seems in favor of the former. The fusion of the outer tissues of the leaf with the stem makes it impossible also to state positively from which segment the sporocarp arises, but I believe it to be the first rather than the second, and certainly it cannot be a younger one than this.

The apical cell of the sporocarp has its longer axis across the leaf, and cuts off segments toward the base and apex of the leaf alternately, to the number of seven or more on each side (*figs. 13, 14*). The exact number of segments formed could not be determined with certainty, but in several cases six and seven pairs were counted, and in others very little older, as shown by their size, apical growth had ceased, and the number of segments was certainly much smaller than in Marsilia, where I found more than twenty pairs of segments. The activity of the apical cell as such is ended when the sporocarp is about a tenth of a millimeter long, by the appearance in it of several irregular anticlines, dividing it up into small cells which soon become indistinguishable from those derived from its later segments, as can be readily seen in a surface view of this part of the capsule (*fig. 15*).

The fate of the segments of the apical cell in the sporocarp is at first exactly like that of the leaf segments (*figs. 13, 14, 16, 17*), but while in the leaf wall III is followed by a pericline that cuts off the protoderm in the marginal cell, it is here followed

by three more section walls. Wall IV is dorsal to the marginal cell and nearly parallel to wall III (*fig. 18*), wall V is on the ventral, and VI on the dorsal side of the marginal cell (*figs. 18, 19*), and the ultimate marginal cell is thus of the seventh grade, just as in the capsule of Marsilia (Johnson '98).

THE STALK.

The type of primary division just given is the one found in most of the later segments of the sporocarp, but in those at the base, which form the stalk, wall IV is often followed immediately by a pericline in the marginal cell which ends its activity as such (*fig. 20*). The further fate of the various sections and the marginal cell is quite similar to that found in the leaf. Procambium, ground meristem and protoderm layers are formed in all; the latter gives rise to epidermis and hypodermis (*e p, h y, figs. 20, 21*), and the ground meristem to the two or three-layered mesophyll and to the partitions separating the small and irregular air canals. We find a notable difference in the fate of the procambium, for the eccentric vascular bundle of the stalk is developed entirely, or nearly so, from the procambium of section I (*a b, fig. 20*), while most of the procambium of the other divisions is devoted to the formation of the large stereome bundle which lies ventral to and partially surrounding the vascular bundle (*s c l, figs. 21, 31–33*). This fuses below with the central stereome of the stem, but ends abruptly above at the basal wall of the capsule. In the mature sporocarp the stalk is sharply curved in ventrally, is smaller at the lower end and considerably enlarged at the upper end where it joins the capsule, at which point also it is peculiarly modified on the dorsal side, as will be described in detail in speaking of the wall of the capsule.

The vascular bundle of the stalk, as Meunier has pointed out, does not fuse with that of the leaf in the way described by Goebel, but usually, according to my own observations, fuses first with the bundle of the axillary bud, and then this composite bundle reaches that of the stem at or near where the leaf bundle joins the latter.

THE CAPSULE.

In the terminal segments of the sporocarp, which form the capsule, the number of primary divisions is seven, as we have seen. Of these the six sections immediately divide up to form the three meristem layers, while the marginal cells, or at least a pair of these on each side, do not (*figs. 19, 22*). There are four ultimate marginal cells in each segment arising from the division of each of the two quaternary marginal cells by a transverse anticline (*fig. 14*). On each side of the capsule we find that two of these cells, in different but successive segments, become considerably larger than their fellows (*fig. 14*), and each finally gives rise to the sporangia of one of the four sori. In several cases these sporangial marginal cells, as we may call them, seemed to be the upper ones of the segments, as in the case figured (*fig. 14*), but the material at hand of this stage was not sufficient to allow me to determine whether this is always true. Neither can I assert positively that all of the sporangia of a sorus come from one marginal cell, but the evidence obtained is such that I feel practically satisfied that further study will show this to be the case. The essential thing, however, and one which is quite certain, is that the sporangia come from marginal cells, in a way that we shall find to be similar to that found in Marsilia, though differing in some details.

In describing further the development of the various structures of the capsule, we shall find it best to take them up separately, and may conveniently begin with the wall developed from the protodermal layer. Soon after apical growth ceases in the young sporocarp, the portion near the tip, that is the region including the four sporangial marginal cells, begins to swell out ventrally and laterally to form the globular capsule (*figs. 25, 31*), and these marginal cells at the same time begin to divide up to form the many sporangial cells of the sori. No tendency to a circinate coiling of the young sporocarp is seen at any time, but growth soon becomes more rapid on the lower side of the ventral protuberance and the original apex is thus pushed far

around dorsally (*A*, *figs. 31–33*), and the sori, which originate in cells having a lateral position (*fig. 14*), come later to have a position such that the soral canals open nearly terminally *figs. 31–33*), thus making the longitudinal axis of these canals nearly parallel to that of the stalk.

On the dorsal side of the sporocarp in the meantime there is formed a small protuberance at the upper end of the stalk (*l t*, *figs. 31, 32*), which is later found to be supported by a mass of thick-walled cells extending inward nearly to the vascular bundle (*fig. 33*). This protuberance, as was pointed out by Russow in *P. minuta*, is apparently homologous with the lower tooth of the capsule of *Marsilia quadrifolia*. Just above this tooth there is a rather narrow, but deep depression (*b p*, *figs. 31, 34*), which according to Russow corresponds to that found between the upper and lower teeth in *M. quadrifolia*, but there is no marked increase in height of the epidermal cells above this that might represent the upper tooth of the Marsilia capsule (see Russow **'72**, and Johnson **'98**).

It was this bending backward of the young capsule, perhaps, which led Meunier to think that the sori were primarily terminal in position, and this may account also for the view of Campbell that one of the valves is developed from the apical cell of the sporocarp, but it is not very difficult to follow out the details of development satisfactorily if the unchanging sagittal plane is used as a guide.

During this change in the general form of the capsule the protodermal layer throughout, beginning on the dorsal side just above the basal pit, divides by periclines into epidermal and hypodermal layers, and then the latter divides again to form inner and outer hypodermis (*e p*, *h y*, *figs. 30, 31*). These layers soon surround the whole capsule (Mettenius **'46**, Hanstein **'66**) except for the stomata, most of which are near the base of the capsule. At these openings both hypodermal layers are wanting, the guard cells being as usual derived from the epidermis (*s t*, *fig. 33*).

The development of these highly specialized tissue layers

has been very carefully studied by Meunier, and I will therefore give only a brief account of their mature structure. The brown walled cells of the epidermis are prismatic in shape, varying in height from one-half to three or four times their diameter, the highest being those at the base of the capsule near the ventral side (*fig. 33*). In the basal pit the epidermis is made up of several layers of irregular thin-walled cells (*figs. 32, 33*), while just above this on the wall of the capsule it consists of a single layer of very short cells (*fig. 33*). On either side of this narrow pit the epidermal cells are quite high, as was shown by Meunier, but, though this author figures transverse sections of this region of the capsule, he does not appear to have discovered the pit in longitudinal sections, and hence apparently failed to appreciate its significance. Scattered about among the epidermal cells of the ripe capsule are many of the persistent basal cells of the deciduous trichomes (*t c, fig. 33*).

The outer hypodermal layer consists of cells with the clear yellowish walls so thickened that the cavity is entirely obliterated except at the ends (*h y*^{1}, *figs. 33–35*). These cells are of quite uniform length and have the thick walls peculiarly modified at about the middle of their length, by the deposit, as Meunier thinks, of a more albuminous substance in this portion of the wall, to form the most prominent of the several "light lines" characteristic of this layer (*l l, figs. 33, 34*). The inner hypodermal layer consists of rather longer prismatic cells with thick walls, and are occasionally divided into inner and outer cells by obliquely transverse walls (*h y*^{2}, *fig. 33*). In the region between the stalk and capsule it is noticed, quite early in the development, that the cells are somewhat smaller than the surrounding ones (*b w, figs. 25, 31*), and the larger number of nuclei makes this quite striking in stained sections of a stage like that from which the latter figure is drawn, even when the power used is so low that the cell walls are not distinguishable. Finally, quite late in the development, one layer of these cells in the lower part of this basal wall become modified in the same manner as the outer hypodermis of the capsule (*fig. 33*), and

is continuous with this hypodermis laterally and ventrally (*figs. 33, 34*). For a narrow space in the dorsal region, however, the outer hypodermis from the dorsal wall of the capsule is seen in sagittal section to continue on down into the stalk, making a sharp bend and becoming much thickened just opposite the basal pit, while the similar layer of the basal wall laps over on to this above and abuts against the thin inner hypodermis (*fig. 33*). Horizontal sections (*fig. 35*) show that the region of overlapping is a very narrow one, and that this arises from the transverse division here of cells which are elsewhere undivided. Whether this division gives rise to an open slit is difficult to determine, but I believe that at maturity there is an actual opening here which may have the function, attributed by Russow to the similar structure in Marsilia, of allowing an interchange of air between the capsule and the air canals of the stalk.

Russow noticed the thinness and the bulging outward of the outer hypodermis just above the basal pit, as shown in horizontal section (*fig. 34*), but was unable to study it thoroughly from lack of material. The course of the light line at the point of overlapping is worthy of special notice. It moves toward the inner surface of the hypodermis (*ll, figs. 33, 34*) and finally passes over into the basal wall (*figs. 33, 35*), and the thickening of the walls of the cells in these layers is seen to be definitely related to this line, the cell cavity increasing in size with the distance out from this line toward the end of the cell (*figs. 34, 35*), while where two layers are present (*fig. 35*), the cells of the outer one, in which the light line is wanting, have very slightly thickened walls. At the stomata also the light line is seen to bend outward to the guard cells, so that we may conclude that this line indicates the distribution of some material which makes the hypodermis impervious to air or moisture, and is therefore present only where needed for this purpose.

At the base of the capsule the inner hypodermal layer is wanting, and is replaced by several layers of brown-walled cells which form the inner portion of the basal wall (*fig. 33*). Next to the prismatic outer layer of this wall these cells are closely

packed together, but farther up many small intercellular spaces occur. These spaces open into the larger spaces between the rounded parenchyma cells surrounding the vascular bundle under the base of the sori, and these in turn connect with the still larger canals in the mesophyll which surrounds the capsule just within the hypodermis (*fig. 33*).

In the region near the basal pit the inner hypodermis seems to be pretty sharply separated from the cells of the inner portion of the basal wall (*fig. 33*), running down from the dorsal side of the capsule as a very thin layer which abuts against the overlapping edge of the outer layer of the basal wall. The cells of the inner portion of the basal wall in this region are thin-walled and have small intercellular spaces between them, suggesting thus the tissue that was described by Russow as filling the "lens-shaped space" in this part of the capsule of Marsilia. There is, however, no indication of a duplication of the hypodermis to shut off these cells from the rest of the capsule (see Russow '72 or Johnson '98), nor is there any trace of the rod of brown cells described by Russow as occupying the anterior end of this lens cavity.

THE VASCULAR BUNDLE SYSTEM.

This system has been carefully studied by Meunier, and since my own work confirms his in all essential points, I have, with his consent, reproduced several of his figures (*figs. 36–38*) of its mature anatomy.

In the development of the vascular system we have already seen that the axial bundle of the stalk comes from section I entirely, and this is true also of the simple continuation of this bundle into the capsule (*a b, fig. 24*). The rapid modification in shape and position of the various parts of the capsule, however, makes it practically impossible to trace out the origin of the many branches in the capsule with reference to segments and meristem layers, as it was possible to do in Marsilia.

After penetrating unbranched nearly to the base of the sori (*fig. 33*), the axial bundle divides, sending one branch to the

right side of the capsule and one to the left, forming a short transverse bundle perpendicular to the main trunk (*tb*, *figs. 36, 37*). Each end of the transverse bundle soon divides again, sending one branch upward and dorsally in each case, and the other downward and ventrally (*figs. 32, 33*). Then each of these four branches, which correspond to what I have called the "lateral branches of the dorsal bundle" in Marsilia, divides to form the three peripheral bundles of its respective valve (*l b f*, *figs. 30, 36, 37*). Of these bundles, the middle one of each valve gives rise, a short distance above its base, to a short branch (*p a b r*, *fig. 36*) that turns abruptly into the capsule to join the placental bundle which runs through the length of the placenta just back of the sporangia (*p a b*, *figs. 30, 36*). Of the other two main branches in each valve, one runs along close to each edge of the latter (*l b f*, *figs. 27–30*), and all three fuse again at the tip of the valve (*figs. 36, 38*). There is never a fusion of bundles from upper and lower sori on the same side of the capsule as occurs in Marsilia, and the absence of this allows the separation of upper and lower valves on each side, just as the absence of fusion across the median plain in Marsilia allows the separation of the wall of the capsule into right and left valves.

THE SORI.

In the young soral segments the growth in a tangential direction of sections II and V is comparatively slight, while the sections dorsal to the marginal cell grow vigorously and thus push this cell around into a nearly ventral position (*m c*^{1}, *fig. 19*), After increasing considerably in size, the marginal cell divides into halves by an anticline parallel to the median wall (*s p c*, *fig. 22*), and then these halves are divided further by walls parallel to the first (*figs. 23–26*) and by others perpendicular to these (*figs. 27–29*), giving rise thus to the large number of sporangium mother cells of the sorus. During the growth and division of these derivatives of the marginal cell they are turned over, by the continued growth of the dorsal sections, so that the originally outer surface finally faces toward the cells of section V, which

have been turned in a similar way to face laterally outward (*s p c*, *fig. 23*). The slight depression thus formed on the ventral surface (*s c*, *figs. 23*, *24*) is the beginning of the soral canal, which grows constantly deeper as the capsule develops (*figs. 24–26*), becoming crescent-shaped in cross section (*figs. 27–30*), and finally closing at the outer end, by the growing together of sections V and VI, to completely inclose the sporangial cells (*figs. 26–32*).

By the striking change in the external form of the capsule already mentioned, the position of the sori within this is considerably affected. From their origin (*fig. 14*) we might expect the sori to face the median wall, as in Marsilia, but this is not the case, for in accommodating themselves to the globular form of the capsule, the sori of the upper pair soon come to face inward and downward, while those of the lower pair face upward and inward (*figs. 27–29*), or, in other words, all four face toward the central axis of the capsule.

When fully developed to sporangium mother cells the derivatives of the marginal cells are elongated perpendicularly to the surface of the sorus, densely filled with contents, and have large nuclei in which, in the resting stage, the chromatin is collected in a few rounded masses (*figs. 26–28*). The number of sporangium mother cells in the length of the sorus is ten or more (*fig. 26*), while the number seen in transverse sections varies from four to five at the base or top (*figs. 27*, *30*) to as many as twelve at the middle (*fig. 29*).

The basal cells of the sorus are the first to form sporangia (*fig. 26*), and this begins in each of them by the occurrence of inclined walls, cutting out a tetrahedral apical cell (*s p*, *figs. 26*, *28*, *29*). One or more series of segments are cut off from this, and then a pericline appears at the outer end, completing the sporangium wall and forming the archesporium, which later cuts off the tapetum in the usual way (*s p*, *figs. 28–30*). According to Meunier, who has carefully described the development of the sporangia, the microsporangia and macrosporangia are just alike up to the time of formation of the mother cells. This view is

confirmed by Campbell, and I believe it to be true, though I have not been able to follow out in detail this part of the development.

Among the cells at the base of the sorus, where the first sporangia are formed, are a few cells which do not develop sporangia until much later, so that the sporangia in this region differ greatly in age, and hence in size (*s p*, *fig. 30*). In the middle and upper portions of the sorus there seems to be much less disparity in the size of the sporangia, as all of the sporangial cells form sporangia at about the same time (*fig. 29*). From the similarity in distribution in the sorus of the sporangia first formed to that of the macrosporangia of the mature sorus, one is tempted to believe that these primary sporangia near the base of the sorus are the only ones that develop to macrosporangia, while the backward sporangia, including a few at the base and all those of the upper part of the sorus, give rise to microsporangia only, but this view could not be definitely confirmed.

I can corroborate Campbell's statement that no stalk cell is regularly formed in the development of the sporangia, and whether the cell sometimes seen at the base of the sporangial cell (*fig. 29*) is the homologue of the stalk cell of the Polypodiaceæ seems open to question.

We have seen that while the indusium which separates the sori of the laterally opposite pairs from each other is formed by the ventral outgrowth of sections II and V, that which separates the upper and lower sori of the same side must be derived principally from the sterile marginal cells. The presence of intercellular spaces along the median wall is noticed very early (*i s c*, *figs. 25–27*), and these finally run together to complete the separation of the indusia of the opposite sori. A similar splitting apart begins a little later between the upper and lower sori of the same side.

The fact that these layers of tissue surrounding the individual sori are not originally separate is used by Goebel as evidence for the view that it is not an indusium morphologically, but it seems to me that, just as in Marsilia, the mode of development

by the outgrowth of surface cells favors the opposite view, as has been pointed out by Meunier.

SUMMARY AND CONCLUSIONS.

The leaf of Pilularia develops, like that of Marsilia and many other leptosporangiate ferns, by a two-sided apical cell arising on the right and left sides alternately of the dorsal surface of the stem, near the apex.

The eleven or more pairs of segments formed by this apical cell divide primarily into three sections and a quaternary marginal cell, instead of five and a marginal cell of the sixth grade, as in Marsilia. Each of these four divisions takes part in the formation of all three meristem layers. The sheath of the axial bundle is derived from the procambium and not from the ground meristem as in other ferns. The mesophyll of the mature leaf is of a single layer. Outside of this are the ten air canals, separated both laterally and transversely by perforated partitions, and surrounded externally by the epidermis and hypodermis developed from the protoderm.

No indication of a rudimentary lamina could be found by carefully following the details of division in the terminal segments of the circinately coiled leaf.

The sporocarp of Pilularia is a branch of the leaf, arising in an anterior marginal cell at the base of the latter. It grows by a two-sided apical cell which cuts off six or more pairs of segments, and is then divided up by irregular anticlines. These segments, like those of the sporocarp of Marsilia, form seven primary divisions.

This plan of division found in both genera must, I think, be regarded as a characteristic of the spore-bearing portion of the leaf in their common ancestor. From the absence of a lamina in the sterile leaf of Pilularia, it might be suggested that the sporocarp, which also possesses no lamina, had been derived from a leaf of this type. For phylogenetic reasons, however, we must believe that the leaf of the Leptosporangiatæ, from which the Marsiliaceæ are derived, possessed a lamina, developed

in the same manner as in many other families of the group, and had a petiole more like these same forms in the number of divisions of its segments (see Sadebeck '74). Pilularia, on the contrary, has no lamina, and has a smaller number of divisions in the leaf segments, resembling in this respect certain petioles of Marsilia (Johnson '98), where the number of sections is reduced below the normal. Again, the type of division in the capsule seems to be easily derivable from that of the leaf of Marsilia, for the interpolated section IV of the former seems so plainly to assist in pushing the marginal cell around to the ventral surface, that we can readily believe it to have been added to a leaf of this type for this particular purpose. When all of these facts are considered, it seems evident that, so far as the structure of the leaf indicates, Marsilia is the less modified of the two genera, and resembles the other leptosporangiate ferns more closely, while Pilularia has a leaf very much reduced from the ancestral type. Whether the capsule of Pilularia is derived from one with more numerous sori cannot, perhaps, be profitably discussed until we know the details of development in such forms as *Marsilia polycarpa*, or *M. Aegyptiaca*, and *Pilularia minuta*, where the number of sori is reduced in each genus below that in the forms already studied, but from my own study of *P. globulifera* and *M. quadrifolia*, I am inclined to think the capsule of the latter, like its leaf, is the more primitive of the two. It seems to me that detailed study of the leaf development throughout the Leptosporangiatæ may be expected to give more light on the exact affinities of the Marsiliaceæ with the other families of the group.

In the segments forming the stalk of the sporocarp the protoderm gives rise to epidermis and hypodermis, and the ground meristem to mesophyll and the irregular partitions separating the small air canals, while the procambium gives rise in section I to the vascular bundle and in the other sections to the ventrally placed stereome bundle.

The remaining younger segments of the sporocarp are devoted to the formation of the capsule. In this region two of the ulti-

mate marginal cells on each side are devoted to the formation of sporangia, all of those of each sorus arising from one of these four sporangial marginal cells. The sori thus arise in right and left pairs, one above the other on each side, and are not terminal in origin, as described by Meunier, nor with two sori on the median plane, as indicated by Campbell. These sporangial marginal cells give rise in a way somewhat similar to that found in Marsilia, to the large number of sporangium mother cells of the sori, and are in the meantime surrounded by the more vigorous growth of the other portions of the ventral side of the capsule. By the more rapid growth at the base of the capsule on the ventral side, the openings of the soral canals thus formed are pushed around from a lateral position to become nearly terminal in the mature sporocarp.

The macrosporangia and microsporangia are not derived from different marginal cells, as in Marsilia. The earliest evidence of differentiation found here is in the fact that the first sporangia formed, most of them near the base of the sorus, seem to develop macrosporangia, while the upper and younger ones become microsporangia. Except in this matter of location, the two kinds of sporangia are just alike up to the formation of the spore mother cells.

The outgrowth of the cells of the ventral surface of the capsule gives rise not only to the wall surrounding all of the sori, but also to the so-called indusium which separates the different sori from each other. It seems to me that Meunier is right in saying that the development of this tissue here (as in Marsilia also) is sufficient warrant for calling it an indusium. But we cannot agree with Campbell in regarding these indusia as the inturned edges of leaflets enclosing the sori, since we have no evidence that any structure homologous with the lamina occurs in the capsule.

Of course, the whole question of homology is complicated by the fact that the sporangia of the Marsiliaceæ seem to arise on the ventral surface of the leaf. But if we pass from forms like Asplenium, with sporangia borne near the middle of the

dorsal surface of the leaf, through forms like Adiantum, with sporangia near the edge on the same surface, to Lygodium, where, according to Prantl ('87), the sporangia actually arise from marginal cells, the transition to the Marsiliaceæ, with several sporangia arising from each marginal cell, does not seem to be so very abrupt. The indusium of Lygodium also seems to have a striking resemblance to that of the Marsiliaceæ in some features of its development, and may repay further investigation from this point of view.

The axial vascular bundle entering the base of the capsule divides into two, one branch going to the right and the other to the left side of the latter. Each of these again divides, forming four branches, each of which furnishes the three main bundles of a sorus. The middle one of the three in each case develops a placental branch which connects with the placental bundle present in the axis of the placenta. The three bundles of each sorus fuse together at the tip of the valve, but there is no fusion of the bundles of the upper and lower sori on the same side like that found in Marsilia.

The firm wall of the globular capsule of Pilularia is made up, like that of Marsilia, of an epidermis of thick brown-walled cells with trichomes and stomata scattered among them. Within this are two hypodermal layers, the outer of very thick-walled, regularly prismatic cells, and an inner layer of larger, more irregular, brown-walled cells. Across the base of the capsule is formed the thick basal wall, the outer layer of which is continuous with and exactly like the outer hypodermis and has the same "light line" running through it. Near the dorsal side of the capsule there is a narrow slit through this wall, corresponding to the air passage which opens into the lens-shaped space in Marsilia, but, though a tissue similar to that found in this space is present in Pilularia, it is not cut off from the rest of the capsule by a duplication of the hypodermis.

Just opposite the basal wall there is a depression in the dorsal surface of the sporocarp, and just below this, at the upper end of the stalk, is an outgrowth corresponding to the lower

tooth of the capsule of Marsilia. The upper tooth, which in Marsilia consists simply of elongated epidermal cells, is entirely wanting in Pilularia.

In conclusion, the sporocarp of *Pilularia globulifera* is essentially the equivalent of a Marsilia sporocarp in which the number of sori has been reduced to two pairs, and will probably be found to correspond even more closely in development with those Marsilias, like *M. polycarpa* or *M. Ægyptiaca*, which also have a small number of sori. Morphologically, then, we must in both cases consider the capsule as equivalent to a branch of the leaf in which the marginal cells have been devoted to the formation of sporangia instead of a lamina.

BALTIMORE, MD.

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EXPLANATION OF PLATES I–III.

Abbreviations used.— *A*, apex; *ab*, axial bundle; *ac*, air-canal; *arc*, archesporium; *bp*, basal pit; *bs*, bundle sheath; *bw*, basal wall; *cp*, transverse partition; *D*, dorsal; *d*, protoderm; *dw*, protoderm-wall; *ep*, epidermis; *F*, sporocarp; *ha*, halving anticline; *hy*, hypodermis; hy^1, outer hypodermis; hy^2, inner hypodermis; *id*, indusium; *isc*, intersoral cavity; *L*, leaf; *lb*, lateral branch of vascular bundle; *lbf*, fork of the lateral branch; *ll*, light line; *lp*, longitudinal partition; *lt*, lower tooth; *mc*, marginal cell; mc^1, mc^2, etc., marginal cell of the first, second, etc., grade; *mp*, mesophyll; *mw*, median wall; *pa*, placenta; *pab*, placental bundle; *pabr*, placental branch; *pb*, ground-meristem; *pc*, partition cell; *pl*, procambium; *plw*, procambium-wall; *pp*, pores in partition; *S*, stem; *sc*, soral cavity; *scl*, stereome bundle; *sp*, sporangium; *spc*, sporangial cells; *st*, stoma; *sw*, segment wall; ta^1, first transverse anticline; *tc*, trichome; *tp*, tapetum; *tr*, trachea; X, apical cell; I, II, etc., first, second, etc., section walls.

All figures are camera drawings from microtome sections, except *figures 36–38*, which are copied from Meunier.

PLATE I.

FIG. 1. Transverse section of stem through apical cells of two young leaves. × 400.

FIG. 2. Ventral surface of tip of young leaf. × 400.

FIG. 3. Lateral surface of same. × 400.

FIG. 4. Part of transverse section of young leaf. × 400.

FIG, 5. Similar section of an older leaf. × 400.

FIG. 6. The same still older. × 400.

FIG. 7. The same older than the last. × 400.

FIG. 8. The same still older than the last. × 400.

FIG. 9. Similar section of nearly mature leaf. × 75.

FIG. 10. Part of tangential section of a young leaf through the partitions and air-canals. × 200.

FIG. 11. Similar section of older leaf. × 200.

FIG. 12. Part of transverse section of stem showing ventral surface of a young leaf and the mother cell of a sporocarp. × 400.

FIG. 13. Dorsal surface of tip of a young sporocarp. × 400.

FIG. 14. Ventral and lateral surface of the same. × 400.

FIG. 15. Surface view of the apex of an older sporocarp, showing the fate of the apical cell. × 400.

FIG. 16. Part of a section of the tip of a young sporocarp, which cuts the segment on the right parallel to the upper and lower segment-walls and the segment on the left perpendicular to these. × 400.

FIG. 17. Part of a transverse section of a young sporocarp. × 400.

FIG. 18. Similar section of slightly older sporocarp. × 400.

FIG. 19. Part of transverse section of a capsule showing ultimate marginal cell. × 400.

PLATE II.

FIG. 20. Transverse section of stalk of sporocarp. × 400.

FIG. 21. Similar section of an older stalk. × 300.

FIG. 22. Transverse section of a capsule older than that shown in figure 19. × 400.

FIG. 23. Similar section slightly older than the last. × 400.

FIG. 24. The same still older, though lower sori. × 400.

FIG. 25. Approximately horizontal section through upper pair of sori of a capsule considerably older than that shown in figure 31. × 200.

FIG. 26. Part of similar section slightly older, showing formation of sporangia. × 400.

FIG. 27. Part of a section transverse to the sori of a capsule of the age shown in figure 31, near the ventral surface. × 400.

FIG. 28. Similar section of right upper sorus a little older. × 400.

FIG. 29. Similar section near the middle of left upper sorus still older. × 175.

FIG. 30. Similar section, near the base of lower right hand sorus, older than last. × 175.

PLATE III.

FIG. 31. Approximately sagittal section of a young sporocarp, just at the right of the median plane. × 400.

FIG. 32. A similar section of a much older sporocarp. × 200.

FIG. 33. Nearly median sagittal section of a mature sporocarp. × 30. (At *lbf*, in dotted lines, the vascular bundles which would be seen in a section a little farther from the median plane than this.)

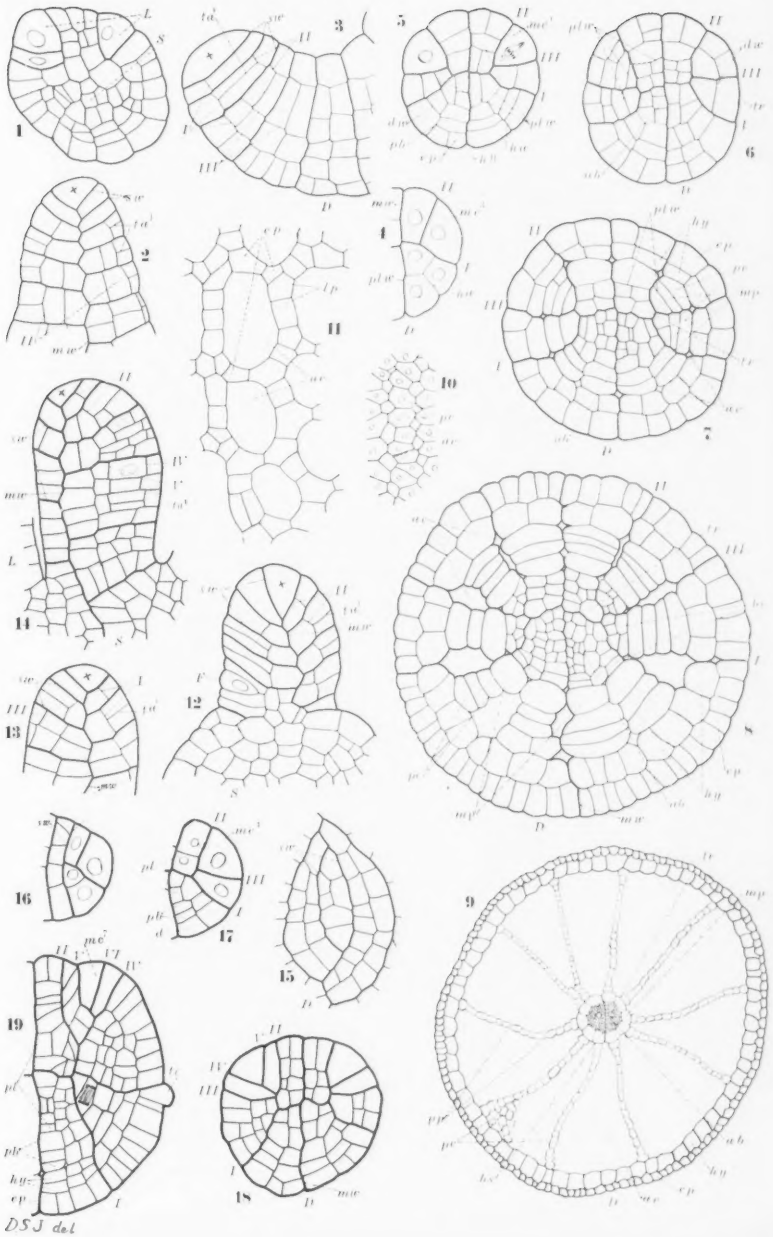
FIG. 34. Horizontal section through pit and base of mature capsule, just dorsal to slit in basal wall. × 175.

FIG. 35. Section parallel to last through slit in basal wall. × 175.

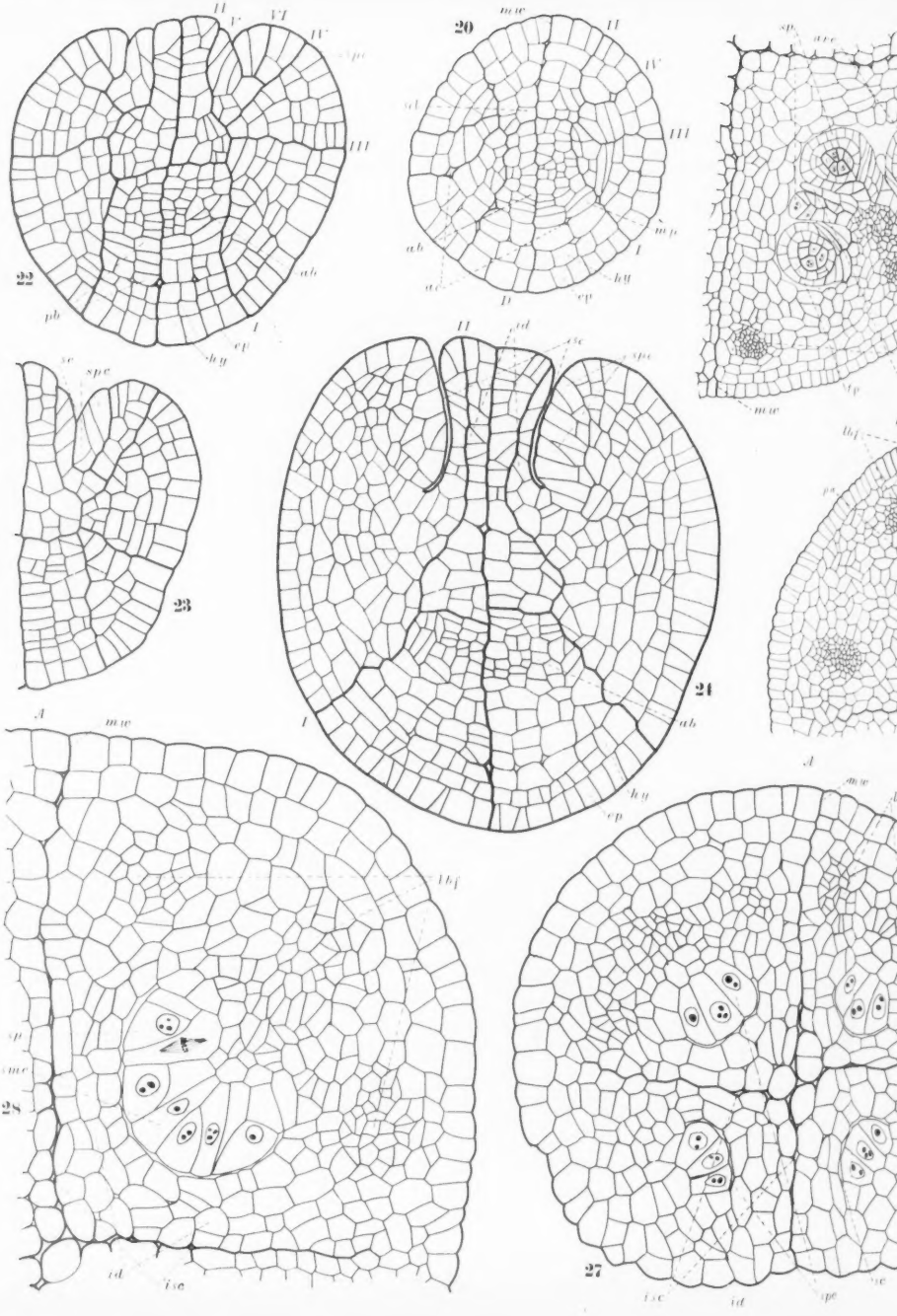
FIG. 36. View from the ventral side of the vascular bundle system of the mature capsule. × 15. (The arrow indicates the direction of the median plane.)

FIG. 37. View from above of the transverse bundle at the base of the capsule and its branches. × 15.

FIG. 38. View from above of the bundles at the top of the capsule. × 15.



JOHNSON on PILULARIA.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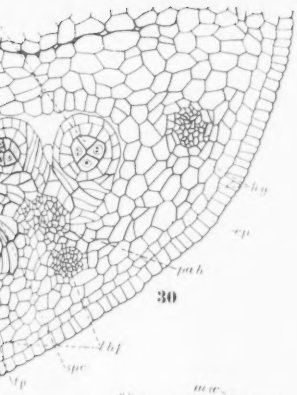
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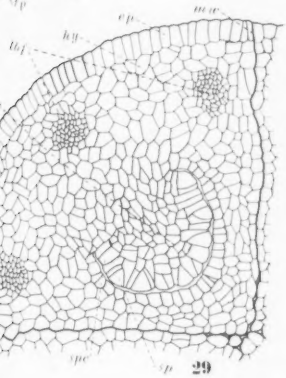
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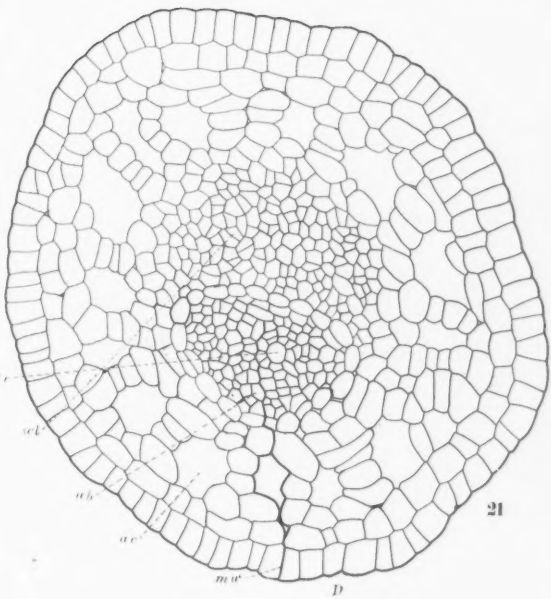
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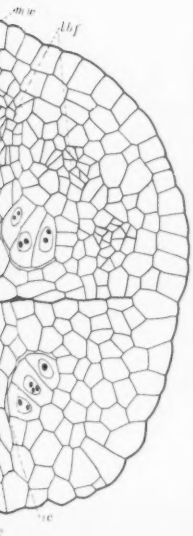
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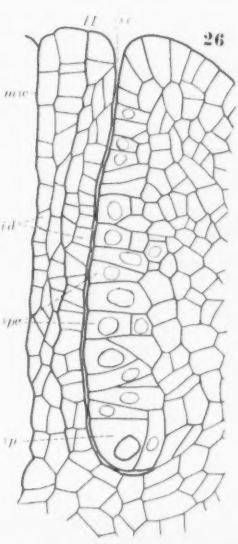
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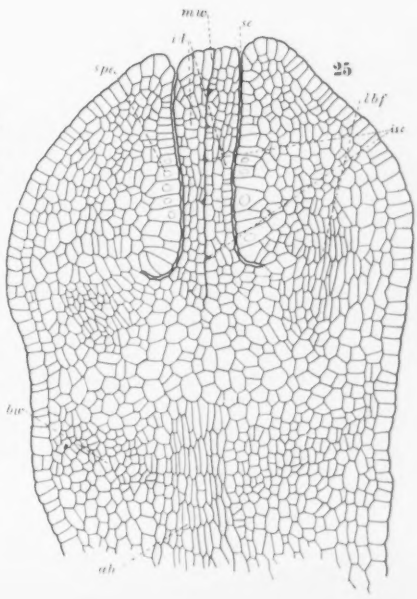
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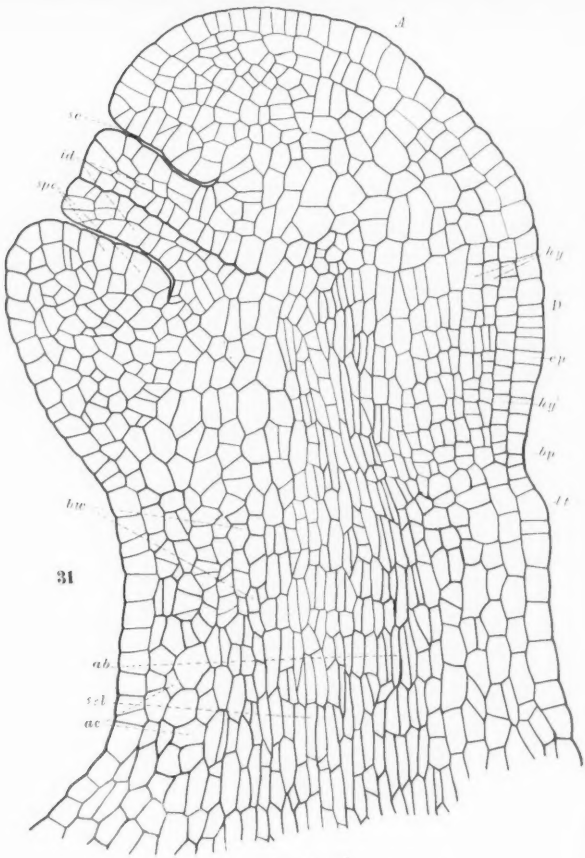

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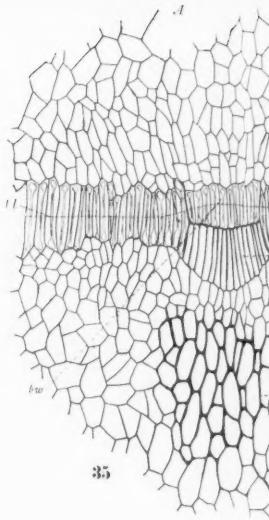

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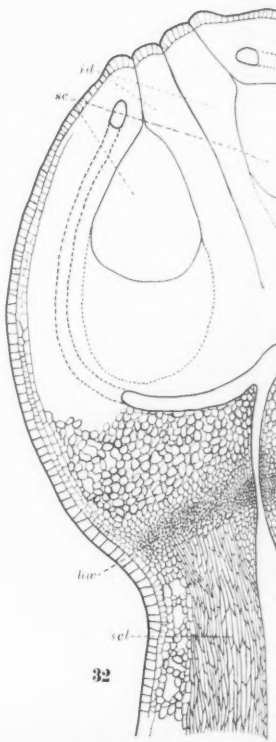

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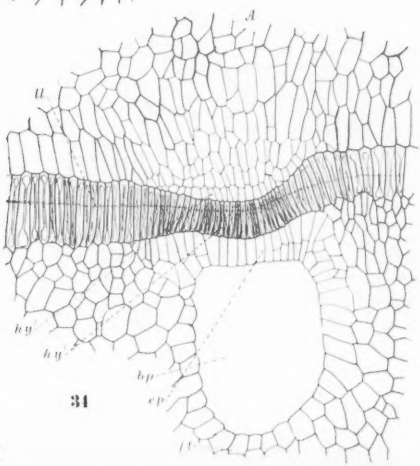

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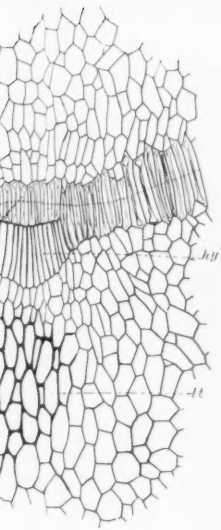

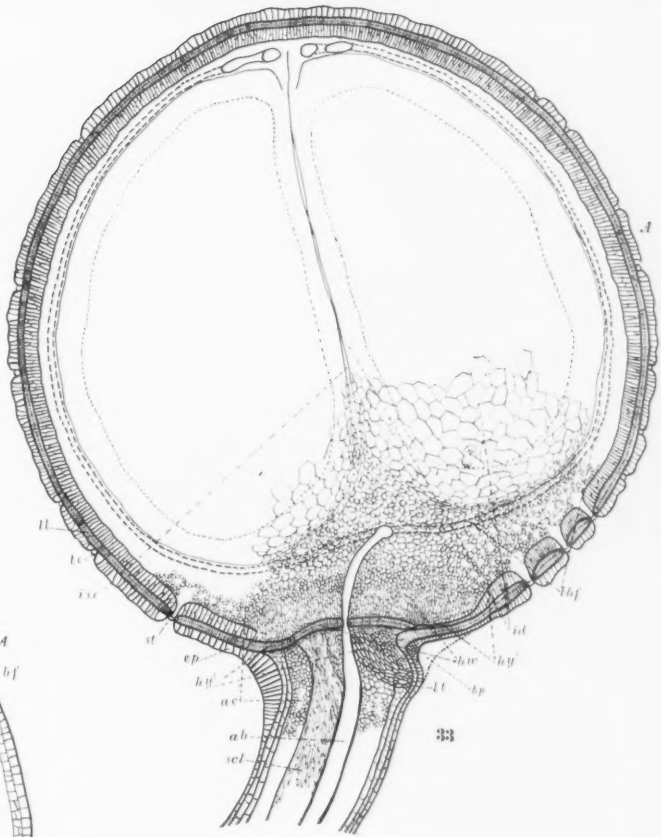

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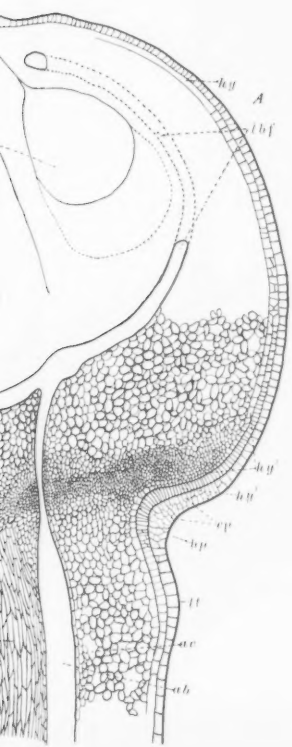

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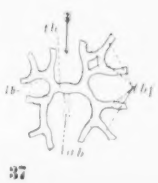

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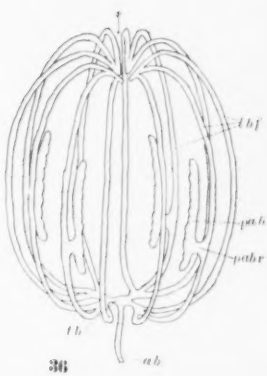

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SON ON PILULARIA.

CONDITIONS FOR THE GERMINATION OF THE SPORES OF BRYOPHYTES AND PTERIDOPHYTES.

FRED DE FOREST HEALD.

(WITH PLATE IV)

I. INTRODUCTION.

THE investigations upon the effect of light on the germination of fern and moss spores have led to opposite and contradictory results. According to Borodin, Schmidt and others, the failure of fern spores to germinate in the dark is experimentally demonstrated, while Göppert and Schelting arrived at exactly opposite conclusions. Leitgeb has shown the necessity of light for the germination of liverwort spores, and Milde succeeded in germinating Equisetum spores in the dark. Up to this time no systematic work on the germination of moss spores in light and darkness has been carried out. In order to clear up this existing confusion and extend our knowledge in regard to the conditions for the germination of moss spores, the present investigation was undertaken.

Before proceeding with the results of my own experiments however, I will treat a little more in detail the investigations bearing upon this subject, which have been hitherto published.

II. HISTORICAL.

The early botanists were in no sense of the word physiologists, and so from the time when the spores of mosses were first observed and compared to the seeds of flowering plants nearly to the present time, their germination has been treated almost exclusively from the morphological point of view. A historical summary of the works on the germination of the spores of Musci and Hepaticæ, up to 1884, is brought together by Lind-

berg.[1] The summary is not quite complete, as no mention is made of the result which Borodin[2] obtained with spores of *Polytrichum commune*. He found that they were unable to germinate in darkness. The work of Müller-Turgau[3] on the germination of spores and the production of secondary protonema is also omitted.

As regards the fern spores, the earlier investigators made the assertion that light prevents their germination, as is to be noted in the works of Senebier, Humboldt,[4] Ingenhouss,[5] and Treviranus.[6] More recent investigators, as Kaulfuss,[7] Leszczye-Suminski,[8] Merklin,[9] Wiegand[10] and Hofmeister,[11] intimate that light is one of the necessary conditions for germination, although no definite investigations in that line are mentioned.

The first investigations of importance from the physiological point of view are those of Borodin.[12] He experimented with eight different species of ferns and found that in all cases light was necessary for germination, and that in the dark no bursting of the exine occurred. His experiments are lacking in one datum, since he does not state at what temperature the cultures were kept. As shown by my own investigations this is one of the most important points. Two years later Göppert[13] succeeded in bringing the spores of Osmunda to germinate in the dark, but the temperature at which the cultures were grown is unknown to me. A year later, Schmidt,[14] with cultures of the spores of *Aspidium violaceus* and *filix-mas*, confirmed the results previously

[1] Historiska Data rörande vår Kännedom om Moss-sporens Groning. Helsingfors, 1884. Rectorprogram.

[2] Bull. de l'acad. imp. de S. Petersbourg, **12**: 433–440. 1867.

[3] Arb. d. Bot. Inst. zu Würzburg **1**: 475–499.

[4] Aphorismen 90.

[5] Versuche mit Pflanzen II. 5. Abschnitt.

[6] Physiologie der Gewächse **2**[2]: 584. 1838.

[7] Das Wesen der Farnkräuter 59. 1827.

[8] Zur Entwickelungsgeschichte der Farnkräuter 8. 1849. Berlin.

[9] Beobachtungen am Prothalium der Farnkräuter 5. 1850.

[10] Entwickelungsgeschichte der Farnkräuter. Bot. Zeitung **7**: 17. 1849.

[11] Vergleichende Untersuchungen 78. 1851. [12] *Ibid*, 529–541.

[13] Schmidt, Über einige Wirkungen des Lichtes auf Pflanzen 21. 1870. Breslau.

[14] *Ibid*, p. 20.

obtained by Borodin. In 1872 Kny[15] obtained results which contradicted those of Göppert for Osmunda spores. The next work of importance was that of Schelting[16] in 1875. He investigated the spores of four different species and found that in all cases germination occurred in the dark. One of the species which he used, *Ancimia Phyllitidis*, was also used by Borodin in the investigations above cited. I have not had access to the original paper, but the probability is, from the review, that the cultures were kept at a temperature higher than the normal room temperature.

Again later, G. Beck[17] has shown that the spores of *Scolopendrium vulgare* germinate only when exposed to light.

Milde[18] and Sadebeck[19] have shown that the spores of Equisetum germinate in the dark as well as in the light; while Leitgeb[20] in his excellent work on the liverworts has shown that darkness prevents the germination of the spores; also that faint illumination causes the development of protonemata which differ markedly in form from those grown under normal illumination. With this short historical summary as an introduction I proceed to the results of my own investigations.

III. EXPERIMENTAL.

The majority of the cultures were made either upon filter-paper, pieces of flower pots, or earth placed in Petri dishes and carefully sterilized. Any special methods will be described in connection with the experiments themselves.

1. MOSS SPORES.

First as to the experiments with moss spores. Cultures of *Funaria hygrometrica* spores were made, and in one case exposed to normal illumination, and in another placed in the dark cham-

[15] Jahrb. f. wiss. Bot. **8**: 4. 1872.
[16] Bot. Jahresber. **3**: 328. 1875.
[17] Bot. Zeitung **36**: 780. 1878.
[18] Nova Acta Acad. L. C. F. **23**: 2.
[19] Bot. Zeitung **35**: 44, 45. 1877.
[20] Sitzungsber. d Akad. d. Wiss. Wien. **74**: 1. 1876.

ber; both being kept at a temperature varying from 19–21° C. At the end of three days the spores exposed to light had germinated abundantly, while those in the dark chamber showed no signs of germination, not even a bursting of the exospore. The dark culture was kept for a month, and at the end of that time there was no indication of germination. That the spores had remained normal and had not lost their power of growth was shown by their speedy germination when exposed to ordinary illumination. This experiment was repeated several times with the same result. Similar experiments were carried out with spores of *Brachythecium rutabulum*, *Bryum pendulum*, and *Mnium cuspidatum*, and all revealed the same dependence of germination upon illumination.

In order to determine which part of the spectrum was effective in producing germination, cultures of spores were placed under double-walled bell-glasses filled respectively with potassium bichromate and ammoniated copper oxide. The cultures included *Funaria hygrometrica*, *Bryum pendulum*, and *Brachythecium rutabulum*. At the end of three days the spores exposed to the less refrangible rays of the spectrum had germinated with as great readiness as under normal illumination, while the cultures in the blue light showed no signs of germination, thus acting the same as in darkness. The spores, although retained in the blue light for over a month, showed no germination whatever. The failure of the spores to germinate in the strongly refrangible rays would seem to throw some light upon the processes which occur in germination. Although the spores form some chlorophyll in the blue light, the photosyntactic processes are not active, and hence it might be thought that germination depended upon the elaboration of new material which can only occur to any extent in the less refrangible rays. That this view is highly improbable is shown by the experiments which follow.

Cultures of spores were made of the three species above mentioned and placed in the light in air free from CO_2, the apparatus being the same as that figured by Pfeffer.[21] The first

[21] Pflanzenphysiologie 1: 191. 1881.

series of experiments in bright light showed that photosyntax was not necessary for germination, since the spores had germinated as readily in the air free from CO_2 as under ordinary conditions. The same result was obtained when the apparatus was exposed to less intense illumination by the interposition of an opaque screen. Under these conditions the photosyntax would be insignificant, and hence it appears evident that germination is independent of that process. The influence of light in germination must be sought, then, presumably in a transformation of food products already present in the spore; these chemical changes being initiated by light, and only by the less refrangible rays. More in regard to the nature of this transformation will be brought forward when later experiments are described.

The question which now presented itself was: Is continued exposure to light necessary to germination; in other words, is there a light induction? In order to determine this point, cultures of spores which had been in the dark for twelve hours were placed in the light and carefully watched for the first signs of germination. After about fourteen hours of illumination the spores showed the first signs of germination, in some cases the exine being burst; a slight protuberance, the beginning of the protonema, was also evident. Half of the cultures were allowed to remain in the light as control experiments, while the other half were removed to the dark chamber to undergo further development. Those spores which showed no beginning of germination before removed to the dark did not germinate in the dark, although they had formed an abundant chlorophyll content. Those spores which had begun to put out a protonemal filament continued their growth somewhat, but the filament was long and slender and did not attain any considerable size on account of lack of plastic material. These experiments were carried out with spores of *Funaria hygrometrica*, *Bryum pendulum*, and *Brachythecium rutabulum*, all with the same result. Essentially the same fact has been shown by Borodin[22] for fern spores.

[22] *Ibid.*, 539.

Leitgeb[23] has shown that for the germination of liverwort spores a certain intensity of light is necessary, and my experiments with moss spores show that the same thing is true, only to a less marked extent. In experiments which I conducted with *Marchantia polymorpha* spores, parallel with the cultures of moss spores, where all were exposed to the light in the middle of the laboratory, the different behavior was very marked. The moss spores germinated in the usual length of time and without any apparent modification due to the weakness of the light. The Marchantia spores, on the other hand, showed a very remarkable retardation in germination, and when germination did occur only a long, narrow filament was produced, which gave no indication of the formation of the thallus according to the ordinary method of growth in sufficiently intense illumination. Other cultures were made and exposed to a much weaker light, a room in the Institute basement with only one window being used. First, cultures were placed on a shelf at a distance of about three meters from the window, then at two meters, and then in the window itself. The cultures at a distance of three and two meters from the window showed a complete failure of the spores to germinate, although they produced chlorophyll to some extent. Those which were grown in the window germinated after the ordinary length of time. That the spores remained capable of germination was shown by the fact that they began growth as soon as they were exposed to normal illumination. These experiments then show that under ordinary conditions of temperature and food supply, the moss spores require a certain intensity of light for germination, but that the required intensity is not as great as in the case of the liverwort spores. These facts were demonstrated for the three species of mosses mentioned above.

Reasoning from the results which I had already obtained with fern spores, a series of experiments was carried out in which cultures of spores were exposed to different temperatures. The failure of the spores to germinate in the dark is due, as has

[23] *Loc. cit.*

already been stated, to the fact that the conditions of temperature, light, etc., were such that certain chemical processes necessary for germination could not be active. The results with fern spores show that heat is able to effect this change as well as light, so that germination may be called forth in complete darkness by subjecting the spores to a higher degree of temperature than the normal room temperature. That moss spores would be affected in the same way as fern spores would seem quite probable, but nevertheless my experiments in this direction have failed to find any temperature at which moss spores will germinate in complete darkness, when supplied with only inorganic material. The temperature to which the general cultures were exposed ranged from 19–21° C. Cultures were made for the following degrees of temperature: 23°, 24°, 27°, 29°, 32°, and 35° C., and in each case in complete darkness. The cultures at 35° C. were kept for four days. At the end of that time no signs of germination were visible, hence they were removed to the light and kept at the ordinary temperature. The failure of the spores to germinate under these conditions showed that they had been killed by the high temperature. The other cultures were allowed to remain in the dark for six days and then removed to the light. The spores subjected to 32° were not killed, but a very marked retardation of germination occurred, since the period required for germination was extended from three days to ten. The cultures that had been kept at 29° also showed a retardation of germination, five days being required after the exposure to light. In the other three series of cultures at 27°, 24°, and 23°, no apparent retardation of germination was noticed when the spores were exposed to light.

The above experiments have shown clearly that a continuous exposure to high temperatures is not sufficient to produce germination of the moss spores in the dark. As suggested by the results obtained by Liebenberg[24] for seeds of Poa, it was thought that perhaps a *change* of temperature might be effective in producing germination. To this end the following experi-

[24] Bot. Centralblatt **14**: 21–26. 1884.

ments were carried out: Two cultures of *Funaria hygrometrica* spores were placed in the dark for twelve hours, then in the thermostat at 41° C. for four hours. The cultures were then removed and one placed in light, the other in the dark, both at a temperature of 19–21° C. After three days the spores in the light had germinated abundantly, but those in the dark showed no signs of growth, although they were kept for two weeks. Similar cultures were exposed to a temperature of 41° C. for three hours with the same result.

Cultures similar to the above were made for *Funaria hygrometrica*, *Bryum pendulum*, and *Brachythecium rutabulum* and exposed to a temperature of 32° C. for twenty-four hours. At the end of this time they were placed at the ordinary temperature, the control experiments in the light, the others in the dark. Those in the light germinated after the usual length of time, but in the dark no signs whatever of germination were noted. Thus, change of temperature is also shown to be insufficient in producing germination in complete darkness.

It is known that ether has a stimulating influence on the production of shoots from certain phanerogams, when under normal conditions none are produced. It might also be supposed that it would act as a stimulus to call forth the germination of spores in the dark. In order to determine this point, a series of cultures was made in which the spores were subjected for different lengths of time to a saturated or partially saturated atmosphere of ether. Cultures of Funaria spores were allowed to remain in the dark for twenty-four hours, in order that they might be in a moist condition, and then placed in an ether atmosphere. In the first case they were exposed to the ether atmosphere for one hour, in the next for two hours, and in the next for three hours. Two cultures were used in each case and as soon as they were removed from the ether atmosphere, one was placed in the light and the other in the dark chamber. The control experiments in the light showed, in the experiments to which a two and three hours' exposure to ether was given, that germination did not take place, and hence that the spores had

been killed by the strong ether atmosphere. In the case of spores which had been in the ether for one hour, germination occurred in the light, but it was considerably retarded. In the dark no sign of germination was noted.

From the above experiments it was quite evident that too strong a dose of anæsthetic was administered. Another series of experiments was therefore conducted in which the spores were subjected to an atmosphere containing less ether. In order to supply the ether atmosphere, one part of ether was mixed with twenty of water. The cultures were then exposed to this atmosphere for one and three hours respectively. Those spores which had been in the ether atmosphere for one hour showed a very slight retardation of germination even in the light, but in the corresponding dark culture no germination whatever was noted. Those spores which had been in the ether atmosphere for three hours showed a very marked retardation, the period required for germination being extended from three to ten days. Those in the dark showed no germination. Another culture was treated in a slightly different way; it was placed in the ether atmosphere for one hour, then in the dark for twenty-four hours, then in the ether atmosphere again for one hour, and from that time on in the dark under ordinary conditions. These cultures were kept in the dark for three weeks with the complete failure of the spores to germinate. In so far as the above experiments are concerned, ether retarded the germination of the spores even in the light, and had no effect upon their germination in the dark.

The non-nitrogenous food supply of spores is in the form of oils or fat. The first change of the fats in germination is apparently a decomposition into glycerin and fatty acid.[25] That the ultimate product from this food supply which is used in the first growth is a carbohydrate in the form of sugar may be surmised. At any rate the failure of the spores to germinate in the dark is due presumably to the fact that conditions are not afforded for the chemical changes which the reserve material

[25] Vines, Physiology of plants 173. 1886.

must undergo before it can be used as plastic material for the growth of the cell. There is a possibility that the failure to germinate may be due to the proteid reserve material remaining in a form which cannot be used. This is, however, not as probable as the view just advanced for the non-nitrogenous reserve food. If the supposition is correct, spores when supplied with organic material in the form which the reserve assumes ultimately in germination might be expected to germinate in complete darkness.

As a nutritive solution the following preparation was made: To 100^{cc} of 0.25 pro mille normal inorganic nutritive solution, 2 per cent. of grape sugar and 1 per cent. of peptone was added, and the whole sterilized on the water bath for one hour. Cultures of Funaria spores were made for both light and dark and supplied with this nutritive solution, as great precautions as possible being taken to keep the cultures sterile. An examination of the cultures at the end of three days showed that the spores had germinated as well in the dark as in the light. The very noticeable feature of this experiment was that under these conditions the protonemata were four or five times as large as when supplied with only inorganic nourishment and grown in the light; also that the cells were crowded with large, irregular starch masses, as shown by the iodine test (see *fig. 2*). The question now was: Is this germination in the dark due to the sugar or the peptone or both? In order to determine this point, the following experiments were carried out:

A 2 per cent. grape sugar solution was made from the 0.25 pro mille normal nutritive solution, and cultures of the Funaria spores made for both light and dark. After three days an examination of the cultures showed that germination had occurred as well in the dark as in the light, thus demonstrating the power of grape sugar alone to call forth germinations in the dark. A 1 per cent. peptone solution was then prepared in the 0.25 pro mille normal nutritive solution, and cultures of Funaria spores made for both light and dark. After three days, these cultures also showed germination of the spores in both light and dark-

ness, with the same increase in size of the protonema as in the case where sugar alone was used. In the cultures with sugar nearly every spore germinated, both in light and in darkness; in the peptone culture in the light also the same, but in the dark the number of spores which germinated was relatively small. The above results had already been obtained when Goebel's preliminary note[26] concerning the same phenomenon appeared.

Similar experiments to the above were carried out for *Bryum pendulum*, *Brachythecium rutabulum*, and *Mnium cuspidatum*. With these species essentially the same results were obtained as regards the germination in light and darkness, but the protonemata showed no increase in size, which was such a noticeable feature in the case of the Funaria spores. In the peptone cultures the number of spores germinating in the dark was rather smaller than for Funaria.

That the germination in the dark is due to the nutritive value of the sugar and peptone is highly probable, but still it might be claimed that osmotic pressure was the active agent. In order to throw some light upon this point, the following experiments were carried out: Spores of *Funaria hygrometrica*, *Bryum pendulum*, and *Brachythecium rutabulum* were placed in culture and supplied with a 0.5 per cent. solution of KNO_3. The cultures in the light showed germination after the usual length of time, but no sign of germination was observed in those which were deprived of light. Experiments with the same results were also carried out for the same species in a 1 per cent. solution of KNO_3. De Vries[27] has shown that the osmotic value of KNO_3 is about double that of grape sugar with equal parts of the gram-molecule, or more exactly, the isotonic coefficient of grape sugar is 1.88. The osmotic value of a 0.5 per cent. solution of KNO_3, or approximately a $\frac{1}{5}$ gram molecule solution, would be about the same as that of a 2 per cent. grape sugar solution, or a $\frac{1}{9}$ gram-molecule. The failure then of the spores to germinate under the above conditions would tend to show that the osmotic pres-

[26] Flora **82**: 75. 1896.

[27] Jahrbücher für wiss. Bot. **14**: 454. 1884.

sure within the spore could not have been the operative force in bringing about germination

The absence of any effect from osmotic pressure was also rendered probable from the experiments in which the spores were supplied with either glycerin or potassium tartrate. Spores of the three species above mentioned germinated readily in 1 and 2 per cent. solutions of glycerin in the light, but in the dark they remained unchanged. Glycerin is a non-nutritive substance for the moss-spores, and at the strength used would be about osmotically equivalent to the sugar. In the 1 per cent. solution of potassium tartrate the spores germinated neither in the light nor dark, but in the 0.5 per cent. solution the growth was the same in the light as in the control experiment. In the dark cultures supplied with 0.5 per cent. potassium tartrate there was a complete failure to germinate. The isotonic coefficient of potassium tartrate is 3.99[28], and consequently the osmotic value of the last solution would not be far from that of 2 per cent. grape sugar. Cultures of spores which were supplied with a 2 per cent. solution of lactose, also non-nutritive for the moss spores, showed the same failure of germination in complete darkness. The spores which were exposed to light germinated however with as great readiness as in the control experiment, where they were exposed to ordinary conditions.

It is known that certain substances like iron chloride and cobalt salts, when used in a solution which is too dilute to be poisonous, exercise an accelerating influence upon the growth of fungi. The substances are non-nutritive, and the acceleration of growth is presumably due to a so-called catalytic action. This fact suggested the possibility of calling forth germination in the dark by means of such substances, and to this end the following experiments were performed: Spores of the species generally used were grown in different strengths of iron chloride: 0.25 per cent., 0.125 per cent. In no case was germination called forth in the dark. In the 0.25 per cent. solution the Bryum and Brachythecium spores germinated neither in light

[28] DE VRIES, *Ibid.* 506.

nor darkness. In the 0.125 per cent. solution, however, the spores germinated abundantly in the light. A series of experiments was also carried out in which the spores of *Funaria hygrometrica* were supplied with a dilute solution of cobalt sulfate, $CoSO_4$. I have shown in my investigations with seedlings[29] that cobalt solutions are extremely poisonous; hence in order to obtain solutions which would not have a toxic action, a very great dilution of the stock solution was required. Sowings of the spores were made for both light and darkness and supplied with $\frac{1}{10000}$, $\frac{1}{20000}$, $\frac{1}{40000}$, and $\frac{1}{80000}$ gram-molecule solutions. In all of the cultures the spores germinated in the light without any marked retardation, but in the dark, the same as in previous experiments, no germination occurred. Thus all of the previous experiments point to the fact that germination in the dark was due to the nutritive value of the sugar and peptone, and not to any stimulating or catalytic action.

It is also interesting to know the minimum amount of sugar which will suffice to call forth germination in the dark. First, cultures of Funaria spores were supplied with $\frac{1}{900}$, $\frac{1}{225}$ and $\frac{1}{135}$ gram-molecule solution of grape sugar and placed in darkness. An examination after three days showed that in the first two dilutions, none of the spores had germinated, while in the $\frac{1}{135}$ gram-molecule solution they had germinated the same as in light under ordinary conditions; and also with the usual increase in size, and with the accumulation of starch. The spores of *Bryum pendulum* also germinated in a solution of the same dilution, but those of Brachythecium required a still stronger solution, only germinating in the dark when they were supplied with $\frac{1}{90}$ gram-molecule. The maximum concentration at which germination can occur is not so important, but results were obtained in this line for a single species. Cultures of Funaria spore were supplied with 5, 10 and 20 per cent. solutions of grape sugar. The first two concentrations allowed germination in both darkness and light, but in the 20 per cent. solution the spores germinated neither in light nor darkness. In the 5 and 10 per

[29] Bot. Gaz. **22**: 143. 1896.

cent. solutions, the protonemata which were formed in the light were perfectly colorless and without chlorophyll.

The great difficulty of obtaining perfectly sterile cultures of moss protonemata upon an organic substratum will at once be evident to all who have ever worked in this line. Goebel[30] was unable to obtain perfectly sterile cultures in his investigations upon *Funaria hygrometrica*. If perfectly sterile cultures could be obtained, it would be possible then to determine whether moss protonemata are able to thrive in the dark, when supplied with organic material, as sugar and peptone. This was the problem which now presented itself for solution and to which my attention was next directed. A considerable number of attempts were made, and at last my efforts met with success. The details of the experiments I will describe in the order in which they were carried out.

The medium for the growth of the spores was made as follows: 200^{cc} of 0.23 pro mille normal nutritive solution; 2 gr. grape sugar; 1 gr. peptone; 1 gr. agar-agar. The mixture was boiled on a water bath for three hours and then filtered, and preparations made in small Petri dishes.

Capsules of Funaria were selected which had the opercula still intact and attempts were made to sterilize them. They were first soaked in water until the water had penetrated them thoroughly and then placed in 1 per cent. formol for different lengths of time. The preparation of the cultures was carried out under all possible precautions against infection, in a chamber which had been saturated with steam. So far as these experiments were concerned it was shown that an immersion in the 1 per cent. formol for a length of time sufficient to kill the adhering germs, also proved fatal to the spores.

In order to preserve the spores and at the same time have the capsules in a sterile condition, I was obliged to resort to another method. The capsules were first dipped in melted paraffin and perfectly coated over, and then placed in the formol. The coating of paraffin thus prevented all penetration of the

[30] GOEBEL, Sitzber math.-phys. Classe k. Bayer. Akad. Wiss. **26**: 462. 1897.

formol into the interior of the capsules. Then, by operating in the chamber which had been saturated with steam, perfectly sterile cultures were obtained.

The Petri dish cultures offered subsequent opportunities for the penetration of molds, even when extreme care was taken, so that cultures which had been kept sterile for several weeks would often be spoiled by the inroads of fungi. The best results were obtained with cultures made in Erlenmeyer flasks.

Cultures of Funaria protonemata were kept in Erlenmeyer flasks from the first of January to the first of May, four months, in perfectly sterile conditions, and in both light and darkness. Parallel with these was a culture started at the same time upon sterilized earth. The mode of growth of the protonemata on the earth agreed with that already described by Schimper,[31] two protonemal axes generally being produced from each spore and growing in opposite directions. There was almost a complete absence of any rhizoid production. Müller-Turgau[32] claims a quite abundant production of rhizoids by Funaria protonemata. After growing for nine weeks the protonemata had produced an abundance of buds, and rhizoids were then produced from the basiscopic cell of the bud.

Mention has already been made[33] of the power of *Barbula muralis* protonema to separate into distinct cells, which are conidia-like and have the power of growing into new protonemata. Sachs[34] speaks of this capability in regard to Funaria protonemata, and Schröder[35] states it as a general principle, that moss protonemata, when cultivated on too dry soil, break up into the separate cells, which are more resistant, and grow into new protonemata under favorable conditions. In case of the leaf protonema of *Barbula muralis* I have shown that this manner of growth cannot be due to desiccation, since the culture was sup-

[31] *Ibid., plate 1.*

[32] Arb. Bot. Inst. Würzburg **1**: 480. 1874.

[33] Gametophytic regeneration as exhibited by mosses 25. Oswald Schmidt, Leipzig. 1897.

[34] Lehrbuch der Bot. 366. 1874.

[35] Unt. Bot. Inst. Tübingen **2**: 15–21. 1886.

plied with abundant moisture. In my cultures of Funaria protonemata on earth this manner of growth was very marked. The cultures were supplied with a considerable amount of moisture, so that the separation into the individual cells could hardly have been called forth by an insufficient amount. In the original culture the spores were sowed in the center of the Petri dish, and after several weeks of growth only covered an area about 2^{cm} in diameter. After ten weeks nearly the whole Petri dish (6^{cm} in diameter) was filled with a luxuriant growth of protonemata, a large majority of which had grown from separate cells.

The cultures in the light on agar-agar produced no buds although they were exposed to sufficient illumination for four months. The control culture on earth had produced an abundance of buds after nine weeks. The growth of the whole protonema was not as vigorous as in the control experiment. *Fig. 4* shows where the original spore cell has started to form a bud by the insertion of an oblique cross wall; further than this, however, no indication of bud formation was noted. The cultures in the dark produced protonemata of considerable size and vigor, but the vigor of growth was markedly below the same cultures in the light. The protonemata were perfectly free from chlorophyll, and the considerable size attained shows that to a certain extent they are able to adapt themselves to a saprophytic mode of nourishment.

In the light the main protonemal axes were directed parallel to the incident rays of light, and grew either in or on the surface of the culture medium. The secondary branches grew erect from the prostrate axes, and directed themselves towards the light at an angle of about 45°, thus exhibiting a marked positive heliotropism. Sachs[36] has already referred to the so-called dorsiventrality of Funaria protonema. In the dark the main axes were without any definite direction, while the secondary branches grew more or less vertical, but irregularly in all directions. Whether this vertical growth of the secondary branches in the dark is due to negative geotropism, I am not able as yet

[36] Vorlesungen über Pflanzenphysiologie 640. 1882.

to state with certainty. Some cultures which were grown in the dark in an inverted position showed that the protonemal branches grew downward, away from the culture medium. These experiments would tend to show that the vertical growth was not due to geotropic sensitiveness, but rather perhaps to negative hydrotropism, as in the case of fungi. More experiments in this line are necessary, however, to make these conclusions certain.

It was thought that by using the culture medium with less peptone the protonemata might be brought to a more vigorous development. A second series of experiments was carried out, in which the same culture medium as described above was used, except that only traces of peptone were added. Even in this medium the protonemata did not grow with their normal vigor, either in light or darkness. The growth was, however, more luxuriant than in the cultures which were supplied with more peptone.

2. MARCHANTIA SPORES.

The work of Leitgeb upon the effect of light on the germination of liverwort spores has already been mentioned. Since he found that the spores were unable to germinate in complete darkness, a confirmation of his results at this point cannot be without interest. A culture of Marchantia spores was kept in the dark for over two months without any signs of germination. At the end of this time they were placed in the light, and after a lapse of six days the majority of the spores had germinated. My experiments also confirmed his results in regard to the intensity of light necessary for germination. In weak light germination was retarded, and when growth did take place the spores produced only a narrow filament, with a small amount of chlorophyll. The filament did not attain any considerable size or form a germ disk.

As regards the part of the spectrum effective in producing germination, my experiments with Marchantia spores yielded the same results as for moss spores, and the same as has been found

for fern spores by Borodin.[37] That is, the blue rays, the more strongly refrangible, have apparently the same effect as complete darkness. In the potassium bichromate light germination occurred after six or seven days, and with every evidence of as vigorous growth as under normal illumination.

The effect of temperature on the germination of Marchantia spores in the dark was also investigated. A series of cultures was made for 32°, 29°, 27°, 24°, and 23° C., and all placed in the dark. After two weeks' time they were observed, and none of the spores had germinated. They were then placed in the light to see if they had remained capable of germination. In the cultures which had been kept at 29° and 32° C. germination was retarded for a few days, but the spores from the remainder of the cultures grew after the usual length of time.

The length of time required for germination, and the condition of the material, rendered the preparation of sterile cultures impossible, so that the cultures with grape sugar were not very satisfactory. Although I did not succeed in bringing the spores to germinate under these conditions, they gave every indication of growth, and I attribute the failure to germinate only to the inroads of bacteria. In the dark in sugar solution the spores increased to three or four times their original diameter and formed large starch masses the same as in the moss protonemata.

Further than this they could not be brought, although repeated attempts were made, and when the cultures were placed in the light even then germination did not proceed, showing that the spores had not remained capable of germination. If, however, the cultures could have been kept sterile, there was every indication that the spores would have germinated.

3. FERN SPORES.

A culture of the spores of *Ceratopteris thalictroides* was kept in the dark for three months without any signs of germination, while a sowing of the same spores germinated in the light after

[37] *Ibid.*, 536.

twelve days. Experiments with the spores of *Alsophila Loddigesii* led to the same results. Thus for the species investigated, it can be stated as certain, that under ordinary conditions of nourishment and at a temperature of 19–21° C. the spores are not capable of germinating. The effect of a higher temperature was then tried for the spores of *Ceratopteris*, a culture of the spores being kept at 32° C. in the dark. After a lapse of sixteen days the culture was examined, and it was found that the spores had germinated abundantly. The form of growth was that of a cell filament, seven or eight cells long, the whole being about 2^{mm} in length (see *fig. 5*). The basal cell always produced a rhizoid, and in some cases the end cells of the prothallium divided also longitudinally. The comparative size and form of a prothallium grown under these conditions and one grown in light at the normal temperature is shown in *figs. 5* and *7*. Experiments of a similar nature were also carried out for *Alsophila Loddigesii*. These experiments are interesting in that they show how Borodin and Schmidt, and Göppert and Schelting could have obtained such contradictory results.

4. EQUISETUM SPORES.

There are no contradictory views in regard to the germination of Equisetum spores, both investigations cited admitting and establishing the fact that germination occurred in perfect darkness. I have repeated these experiments for spores of *Equisetum arvense*, with the same result. It can then be stated with absolute certainty, that Equisetum spores are able to germinate under ordinary conditions of nourishment and at a temperature of 19–21° C., in darkness as well as in light. From the foregoing results it seems that light or organic nourishment is one of the necessary conditions for the germination of moss and liverwort spores, in order that chemical changes may take place which will bring the reserve food material into a condition in which it can be used in growth. For the ferns, these chemical processes may be initiated either by light or a sufficiently high temperature, while in the case of Equisetum these

changes can occur at a much lower temperature in both light and darkness.

IV. SUMMARY.

The more important results of the foregoing investigations may be stated as follows:—

1. Under ordinary conditions of temperature and inorganic nourishment, moss and liverwort spores are unable to germinate in the dark. Spores when subjected to the more strongly refrangible rays of the spectrum only behave the same as in darkness.

2. Organic nourishment in the form of either peptone or grape sugar will call forth the germination of moss spores in complete darkness. Moss protonemata are able to attain a considerable size in the dark, by a saprophytic nourishment, although the vigor of growth is considerably below the normal.

3. Under ordinary conditions of temperature and inorganic nourishment, fern spores are unable to germinate in the dark. A higher temperature, however, will furnish conditions for the germination in complete darkness.

4. The spores of Equisetum germinate apparently as well in darkness as in light and at the ordinary room temperature of 19–21°C.

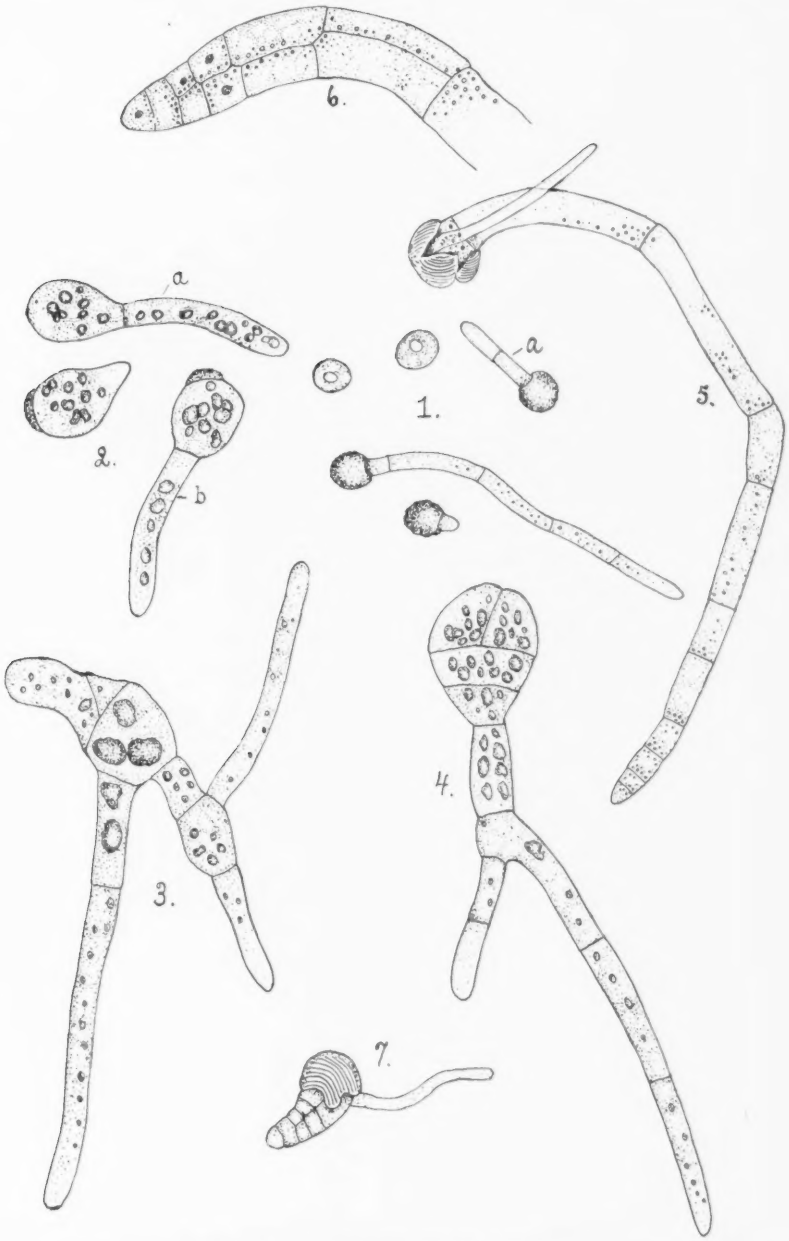
The experiments for this work were conducted during 1896–7 at the Botanical Institute, Leipzig, under the direction of Herr Geheimrat Professor Dr. Pfeffer, to whom thanks are due for many valuable suggestions.

PARSONS COLLEGE,
Fairfield, Ia.

EXPLANATION OF PLATE IV.

FIG. 1. Various stages of Funaria spores, germinated in the light under normal conditions; *a*, after being in culture for three days. × 330.

FIG. 2. Spores of Funaria germinated in the dark in a sugar solution; *a* and *b*, after being in culture for three days. × 330.



HEALD on GERMINATION of SPORES

FIGS. 3, 4. Protonemata of Funaria grown in the dark; eight days on peptone, sugar, and agar-agar. × 330.

FIGS. 2, 3, 4 show a large number of starch masses.

FIG. 5. Prothallium of *Ceratopteris thalictroides*, grown in darkness, at 32°C. In culture sixteen days. × 330.

FIG. 6. Apical portion of a prothallium of the same species, showing longitudinal as well as transverse divisions. × 330.

FIG. 7. Germinating spores of the same age as in *fig. 5*, but grown in light at a temperature of 19°–21°C. × 330.

BRIEFER ARTICLES.

NOTES ON THE GENUS *BARTONIA*.

In August 1894, while collecting near Holyrood, on Conception Bay, Newfoundland, Mr. H. von Schrenk and the writer secured some sixty or more individuals of a Bartonia. These inconspicuous plants were collected in a small sphagnum bog near South Arm river, and in the field were taken for *B. tenella* Willd; but, when later compared with copious herbarium material of this species, the Newfoundland plant was found to differ in several particulars. From its alternate leaf scales and relatively long corolla (twice the length of the calyx), it was then regarded as the *Centaurella Moseri*[1] of Steudel and Hochstetter, and was accordingly distributed as *Bartonia Moseri* Rob. & Schrenk. But before an account of the Newfoundland collecting expedition was published it became doubtful whether the Bartonia was after all identical with the plants of Moser and Drummond upon which *Centaurella Moseri* was founded. Therefore, to avoid making in print the new combination *Bartonia Moseri* based upon indefinite material, the plant was treated as follows:[2]

"Bartonia sp. (*Centaurella Moseri*, Steud. & Hochst., acc. to Griseb., in DC. Prodr. 9: 121). A plant which appears to represent, at least in part, this rare and poorly understood species, was discovered in a small bog near Holyrood (5). The species was first described from specimens collected by Moser at Saltsburg, Pa., and Drummond at Covington, La. In his treatment of the genus in DeCandolle's Prodromus, however, Grisebach includes in it, with the mark of affirmation, a specimen collected by La Pylaie in Newfoundland. As the present plant agrees with Grisebach's description as regards alternate leaf scales and in having the corolla twice as long as the calyx, there can be little doubt that it is the plant of La Pylaie. It is, however, of lower growth, less branched, and less numerously flowered than Drummond's specimen — differences perhaps wholly due to the

[1] First published in Griseb. Gen. et Sp. Gentianearum, 308. 1839.

[2] Robinson & Schrenk: Notes on the Flora of Newfoundland, Canad. Rec. Sci. 1896, p. 20 of reprint.

climate. The flowers, also, are mostly larger and solitary, on peduncles which are often six or nine lines long. From *B. tenella* the Newfoundland plant differs in its alternate leaf scales, loose few-flowered raceme, and relatively larger corolla, which in the fresh state is pinkish; also in its purplish anthers. More perfect material of the United States form of *Centaurella Moseri* is much to be desired."

The combination, *Bartonia Moseri* Rob. & Schrenk, was later published in Britton & Brown's Ill. Fl. **2**: 621, where it is used to cover both the United States material and the Newfoundland plant. Having just received additional specimens of the latter, collected at Grand Lake, Newfoundland, by the Rev. A. C. Waghorne, and in all regards identical with those from Holyrood, the writer has made further study of the plants in question, and is now forced to the conclusion that the Newfoundland form is distinct from any species of the United States. It may be characterized as follows:

Bartonia iodandra, n. sp.—Delicate annual, 4 to 12^{cm} high; root a fascicle of few slender fibers; stem single, erect from a somewhat bent or decumbent base, either quite simple and terminated by a solitary flower, or alternately branched above the middle; branches 0.5 to 3^{cm} long, erect or curved-ascending, being mostly simple leafless peduncles each bearing a solitary terminal flower, but the lowest rarely bearing 2 or 3 flowers; leaf scales alternate, subulate, 2 to 3^{mm} long; flowers at full maturity 6 or 7^{mm} long, distinctly purplish-tinged; calyx turbinate below, its segments ovate-oblong to oblong-lanceolate acuminate; corolla about twice the length of the calyx, when fresh of flesh color, in dried state becoming slightly yellowish but retaining even after several years a suggestion of its erubescent coloration, its segments rather broadly oblong, obtusish and mucronate; anthers at maturity deep purple or dark maroon; filaments broadened below; ovary ovoid, obtuse, surmounted by a thickish sessile short-columnar slightly bilobed stigma which is included within the corolla.—*Bartonia* sp. Rob. & Schrenk, Canad. Rec. Sci. 1896, p. 20 of reprint. *B. Moseri* Rob. & Schrenk in Britton & Brown, Ill. Fl. **2**: 621, as to Newfoundland locality. *Centaurella Moseri* Griseb. in DC. Prodr. **9**: 121, in part (as to pl. of La Pylaie), not Steud. & Hochst.—Collected by B. L. Robinson and H. von Schrenk in sphagnum near Holyrood, Newfoundland, August 23, 1894, no. 5; also by Rev. A. C. Waghorne in bogs near Grand Lake, Newfoundland, August 11, 1897; these stations being nearly 200 miles apart.

B. TENELLA Willd., which is rather widely distributed in the eastern United States, differs from the species just described in having more numerous slightly smaller flowers of a more yellow cast and in well grown individuals borne in many short opposite 1–several-flowered cymes. The corolla is one and a half times the length of the calyx; its segments are narrower and more acute than in *B. iodandra*; the anthers are yellow; the stigma is mostly exserted; and the leaf scales are usually opposite.

Centaurella Moseri Steud. & Hochst. was distinguished from *Bartonia verna* by its still smaller flowers (4^{mm} long) racemosely arranged upon alternate branches, also by its more acutely lobed corolla twice the length of the calyx. The species is represented in herb. Gray by a specimen with the Torrey & Gray label but without data, and by Drummond's specimen from Covington, La., cited in the original description. Both may be merely tall small-flowered specimens of *B. verna*. They differ from *B. iodandra* in stature, inflorescence, considerably smaller flowers, narrower much more acute corolla lobes, and yellow anthers. In formerly classing the two plants together the writer placed too great importance upon the alternation of the leaf scales and the relative length of calyx and corolla—points of resemblance which now seem of less weight than the differences above enumerated, which are probably of specific value.—B. L. ROBINSON, *Gray Herbarium, Harvard University*.

NOTES ON SUNDRY AMERICAN PLUMS.

THE plum section of the genus Prunus is of great interest to American botanists and of still greater consequence to American horticulturists. But even after much careful work by some of our best botanical and horticultural students there are still many difficulties in the delimitation and description of species. The horticulturists have sought to avail themselves of the botanists' classifications, but have found them in many respects inadequate and ill-fitting; and these horticultural difficulties have, to a considerable degree, reacted upon our ideas of the botanical classification of plums, bringing in doubts and complications which would not have occurred to the botanists working by themselves. At the present time the botany and the horticulture of this group are inseparably linked. The horticultural

varieties cannot be classified without a knowledge of the botanical species; and these species cannot be fully understood without a wide study of the cultivated varieties. This is my excuse for calling attention here to some of the species, supposedly among the best known in American botany.

PRUNUS AMERICANA Marshall.—In the absence of Marshall's type specimens his original description makes it impossible to say whether he had in hand the western form which now passes generally under this name, or the northeastern *Prunus Americana nigra*. As long as the two are consolidated after the manner of Gray's *Manual* it makes little difference. If, however, the group is to be divided into two species, according to Sargent's *Sylva* and Britton and Brown's *Illustrated Flora*, it is an open question which part should bear Marshall's name.

PRUNUS AMERICANA NIGRA F. A. Waugh.—This question as to whether our common American plums should constitute one species or two has not yet been fully settled. On the one hand we have Sargent, Britton and Brown, Sudworth[1] and others leaning strongly toward the separation of the two groups; while the Gray publications and the numerous followers of Gray, including Bailey, one of our foremost plum students, hold out for consolidation. It seems to me that, were I unacquainted with the cultivated varieties, I would not hesitate to recognize two species; but the many surprising combinations of *Americana* and *nigra* characters seen in the garden, and the impossibility of disentangling all these varieties, make it more convenient to regard Aiton's group as a botanical variety of *Prunus Americana*. I set forth more fully my reasons for taking this view at the time when I proposed to call this group *P. Americana nigra*.[2]

PRUNUS AMERICANA MOLLIS Torrey & Gray.—Sudworth[3] proposes the name *Prunus Americana lanata* for this variety. No explanation is given for this change, and the variety name of Torrey and Gray seems likely to stand. This variety marks the southwestern evolution of the great *Americana* group, as *P. Americana nigra* is a northeastern modification. The extreme forms are quite as distinct, and by them-

[1] Nomenclature of the arborescent flora of the U. S. Bull. 14, U. S. Dept. Agr., Div. Forestry.

[2] Bull. Vt. Exp. Sta. 53: 60. 1896.

[3] Op. cit. 237. 1897.

selves might readily be described as a separate species. T. V. Munson, an experienced horticulturist and botanist in whose observations I have great faith, has taken this view, and has called the group *Prunus australis* (ined.). This variety is supposed to have a distinctively southern distribution, and it does in fact represent exclusively the species at the extreme south; but the woolly pubescent-leaved specimens are mixed with the smooth leaved plants through northern Texas, Oklahoma and southern Kansas, and probably over a much greater range. The horticultural variety Wolf, which belongs distinctively to this group, originated in Wapello county, Iowa,[4] and the variety Van Buren, also characteristically pubescent, originated in the same state. This matter of distribution is especially interesting in connection with the examination of Scheele's *Prunus rivularis* (see below).

THE HORTULANA GROUP.—The species *Prunus hortulana*[5] was proposed by a horticulturist chiefly to clear up a cloud of horticultural difficulties. Further study of wild and cultivated plums has convinced Bailey[6] that this is "a mongrel type of plums, no doubt hybrids" of *Prunus Americana* and *P. angustifolia*. This view appears to me to be much the best one to take of the *hortulana* plums, as I have taken occasion to explain a year ago.[7] The *hortulana* group is so large and contains so many distinct types that one does not get an intelligent idea of it when it is lumped off as a single species, coordinate with *Prunus Americana* and *P. angustifolia*. As soon as we view it as a group of hybrids we can account for the several more or less distinct subgroups. The best marked types in the *hortulana* group are the Wildgoose type, the Wayland type (see below), and the Miner type (*P. hortulana Mineri*, Bailey). The relations of these groups I have already discussed in the article referred to above. One group, however, is of special interest. This is the one which I have characterized as the Wayland group.[8] Credit is due to T. V. Munson[9] for calling attention to the distinctness of this group, and for referring it to Scheele's *Prunus rivularis*. I have given in another article[10] my

[4] L. H. BAILEY, Bull. Cornell Exp. Sta. 38: 14.
[5] L. H. BAILEY, Garden and Forest 5: 90. 1892.
[6] Cornell Exp. Sta. Bull. 131: 170. 1897.
[7] Garden and Forest 10: 340. 1897.
[8] Ann. Rep. Vt. Exp. Sta. 10: 103. 1897.
[9] Catalogue, 1896.
[10] Garden and Forest 10: 350. 1897; see also Ann. Rep. Vt. Exp. Sta. *loc. cit.*

reasons for including the varieties of this group with the great company of *hortulana* hybrids and for rejecting the supposition of a *Prunus rivularis* derivation. Further investigation confirms me in my earlier view, but leads me at the same time to the belief that Munson was correct in identifying the Wayland varieties with Scheele's *P. rivularis*. In other words, I am convinced that *P. rivularis* Scheele is nothing more than one of the more distinct subdivisions of the multiform *hortulana* group. A part of the argument for this conclusion is already set forth in the article referred to, giving the geographical origin of the varieties of the Wayland subgroup. That is, such varieties as Golden Beauty, coming from the range of the supposed *P. rivularis*, and almost certainly identical with that supposed species, are conspicuously like such other varieties as Cumberland, Garfield, Kanawha, Leptune, Missouri Apricot, Moreman, Sucker State, and Wayland, which have originated respectively in the states of Tennessee, Ohio, Kentucky, Arkansas, Missouri, Kentucky, Illinois, and Kentucky. All these varieties agree fairly well with Scheele's description of *P. rivularis*. If there were such a species it would be almost impossible to exclude all these varieties, and quite impossible to include them all, because we cannot suppose a distribution of *P. rivularis* through the states named.

Moreover, an examination of the material in herbaria passing as *Prunus rivularis* seems to support this conclusion. Scheele founded his *P. rivularis* upon Lindheimer's 389 in *Exsiccata Flora Texana*. Through the kindness of the curator I have been enabled recently to examine the material in the National Herbarium, including a specimen of Lindheimer's 389. This specimen is not an extra good one, but shows flowers, fruit, leaves, and some small twigs, giving most of the characters fairly well. It is a trifle Chicasaw-like in general appearance, but answers nicely in every particular to Bailey's description of *P. hortulana*. It also looks most like Golden Beauty and some other varieties belonging distinctly to the Wayland group. This specimen was collected in 1846, and it seems strange that a greater number of specimens have not been collected since then.

Another specimen in the National Herbarium is 187 of Elihu Hall, and was collected at Dallas in 1872. This one is still more easily referred to the *hortulana* group. In fact it conforms much more readily to our ideas of *P. hortulana* as represented in literature and in herbarium material than do many of the cultivated varieties which

have gone unquestioned into this group. Wright's 181 in *Plantæ Wrightianæ Texano-Neo-Mexicanæ* is referred to *P. rivularis* by Gray,[11] who says, however, "verging to *P. Americana;*" and this specimen in the National Herbarium is transferred to *P. Americana* "fide Sargent, 1892," which shows how equivocal are the current notions of *P. rivularis*. This is, however, a very interesting and puzzling specimen having broad oval leaves, with irregular shallow obtuse obscurely glandular crenulations. Still another specimen which has sometimes been referred to *P. rivularis* is one collected by J. Wolf in Illinois in 1875. This is quite doubtful. In the National Herbarium it is marked "*P. hortulana*, fide Sargent, 1892." The leaves of this are small and shining, with a fine downy pubescence on the young twigs and petioles. But this pubescent character, which is important in the Wayland group, is not at all so marked as among the Wayland varieties proper. Another specimen, sometimes named *P. rivularis*, is that of Thos. Bassler from Manhattan, Kan., 1883. This is a poor specimen, with only flowers and twigs, but is unquestionably *P. Americana*.

The characters of the Wayland varieties, as well as of the *Prunus rivularis* material, are such as would suggest hybridity between *P. angustifolia* and *P. Americana mollis*. Especially the pubescent nature of the petioles and of the veins on the backs of the leaves indicates the parentage of *P. Americana mollis*. The general shape of the leaves and the character of the serratures also point in the same direction. As already pointed out, the distribution of the Wayland varieties almost exactly corresponds to the joint distribution of *P. angustifolia* and *P. Americana mollis*. T. V. Munson, in private correspondence assures me that, in extensive travels through western Texas, he has quite uniformly found an abundance of Scheele's *P. rivularis, i. e.*, plums of the Wayland class, and, distributed everywhere with these, *P. australis* (*P. Americana mollis*) and *P. angustifolia*. He writes me also that he has grown hundreds of seedlings from this wild stock along with the cultivated varieties and their seedlings, and that the group is quite homogeneous and distinct.

Thus it seems probable that Scheele, who, perhaps, had no personal acquaintance with plums in America, and who had a comparatively small amount of material in Lindheimer's 389, gave specific rank to a group which American botanists would not have mentioned separately, and which American horticulturists would have classified immediately

[11] Pl. Wright. Tex.-Neo-Mex. 67. 1850.

by reference to recognized pomological groups. If, however, *P. rivularis* is to stand, the date of its publication would give it precedence over *P. hortulana* for that part of the *hortulana* plums represented; but in view of the tendency to abandon *P. hortulana*, this does not appear to be of very much consequence.

It is interesting to note in this connection that *Prunus Texana*,[12] which Scheele erected at the same time as *P. rivularis* from some more Texas material, has not been heard from since, except to be consolidated with the latter by Sereno Watson.[13]

PRUNUS WATSONI Sargent.—Quite a number of cultivated forms of this species, some of them named and catalogued by nurserymen, have recently come under my observation.[14] I have also examined a quantity of herbarium material. It appears to me that it will be very difficult to draw the line between this species and *P. angustifolia*. Even when Sargent's unabridged descriptions of the two species are placed in parallel columns and diligently scrutinized they will be found to yield but a single character of distinction. The calyx lobes of *P. angustifolia* are said to be glandular-ciliate; while of *P. Watsoni* they are said to be eglandular-ciliate; but this distinction cannot be safely applied to the cultivated varieties, as I have had sufficient opportunity to observe. *P. Watsoni* is usually dwarfer, with more zigzag ashy-gray twigs, and with more appearance of thorniness, and usually has smaller leaves with more finely crenulate margins; but none of these characters will serve for critical discrimination. It may even be found necessary in the future to abandon *P. Watsoni* or to reduce it to a variety of *P. angustifolia;* but for the present this species, name, and description seem to be useful in calling attention to a neglected and very interesting group of native plums.— F. A. WAUGH, *Experiment Station, University of Vermont.*

TWO NOTEWORTHY OAKS.

(WITH PLATES V AND VI)

I. A NEW HYBRID.

FOR three seasons I have been observing an oak which grows in the damp sandy woods near the village of Thornton, Ill., six miles

[12] Beiträge zur Flora von Texas. Linn. **21**: 593. 1848.

[13] Bibl. Index. N. A. Bot. 307.

[14] "The Sand Plums," Country Gentleman **63**: 68. 1898.

south of the southern limits of Chicago. The difficulty experienced in bringing this type of oak under any described species early led to a suspicion of hybridity, and further observations have confirmed this view. The fact that oaks hybridize somewhat readily is strongly in favor of such a solution, when one or two isolated trees are found in the midst of well-marked species of the ordinary kinds. I find no record of a cross between *Quercus palustris* Du Roi and *Q. coccinea* Wang., which evidently takes places here. Dr. Engelmann[1] reported a hybrid of *Q. palustris* and *Q. imbricaria* found near St. Louis about 1870, an account of which was also given by Alexander Braun.[2] This appears to be the only case hitherto noted of any hybrid of *Q. palustris*. It is so much more nearly allied in the character of its leaves to *Q. coccinea* than to *Q. imbricaria* as to add to the difficulty of distinguishing a cross between the two if the leaves only are taken into account, and reliance must therefore be placed principally upon other distinctions, though the color of the autumn leaves is a clear gain. This is the only section near Chicago where I find *Q. palustris*, and it appears to reach its northern limit near the southern end of Lake Michigan here, extending eastward into Indiana and southward in Cook and Will counties, Ill., along Thorn creek and it branches. *Q. coccinea* is more abundant than usual in the woods where the hybrid is found and more sharply defined from *Q. velutina* than customary here. Although there are some features that might be better defined by an assumption of a cross of *Q. palustris* with the latter, the acorns and the autumn leaves are much better explained by a cross with the former. In habit and appearance of the trunk the hybrid is so nearly like *Q. palustris* as at first to have been taken for it. It is a tree of recent growth, 4^{dm} in diameter and about 13^{m} high. The characters are as follows:

Top oblong, the limbs spreading, the lower drooping. Bark of trunk dark gray-brown, tinged with green, close and rather smooth, divided into narrow longitudinal plates, $5–15^{cm}$ long by $2–3^{cm}$ wide. Inner bark coarsely cellular, reddish, colored about like that of *Q. palustris*. Young shoots pubescent, becoming smooth or nearly so in autumn. Branches of the first year brown, tinged with yellow, with small, scattered, slightly raised lenticels. Older branches gray, tinged with red. Winter buds ovate-conical, obtusish, slightly angled, $4–6^{mm}$ long, pubescent with pale or white hairs. Bud scales oval, obtuse,

[1] Botanical Works 405.

[2] Bot. Zeit. **29**: 202. 1871.

brown or with brown margins. Leaves, when bursting from the bud, densely whitish pubescent. As they expand they spread on rather long petioles like those of *Q. coccinea*, and are thin, light green, and soon smooth above, densely white puberulent beneath, retaining the pubescence longer than on the upper surface. Mature leaves in outline broadly oval or some slightly obovate, 9–12^{cm} long and nearly as wide. They are a light glossy green above, lighter and slightly yellow tinged beneath; smooth except tufts of webby hairs in the axils of the principal veins below, mostly confined to the axils of branches of the midvein. They are divided by two deep rounded sinuses on each side, which extend one-half to two-thirds of the way to the midrib. The lobes, except the basal, are somewhat broader above. The lobes are trilobed with shallow rounded sinuses, the terminal lobules three-toothed, the lateral one to three-toothed. The divisions all end in a bristle 4–7^{mm} long. The base of the leaves is truncate or slightly cuneate. Petioles slender, 3–4^{cm} long. Autumn leaves purplish, or spotted with purple, red, or yellow, or many of the leaves scarlet. Male catkins 5–8^{cm} long, hairy; stamens 4 or 5, anthers oblong-oval, retuse or blunt; calyx hairy, 2–4 parted or lobed, frequently 3-parted; segments oval to broad oval or often roundish; they are usually tinged with purple or red. Calyx of the female flower tubular, hairy, tinged with red, six-lobed or cleft. Styles three-parted; stigmas thick, dark and two-lobed. Scales at base of the flower membranaceous. Acorns single or in pairs on peduncles 5–10^{mm} long. The cup is cup-shaped, covering about half the nut, rather thick, contracted at the edge into a thin border, and is yellowish within. Cup scales ovate-oblong, rounded at the apex, slightly pubescent, pale umber colored, with thin margins. When dry they are sometimes loosened near the margin of the cup. Nut globular-ovate, 17–20^{mm} long, 15–17^{mm} wide, pale cinnamon-brown to chestnut color, slightly pubescent, sometimes striped with darker lines.

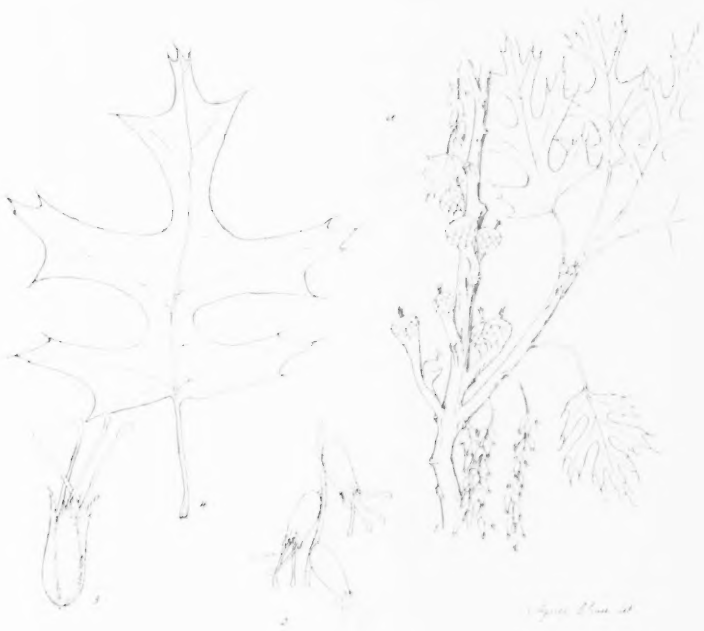
II. A TERATOLOGICAL SPECIMEN.

Farther south in the vicinity of Glenwood is a group of three oaks near the bank of Thorn creek. These have proved of special interest on account of their teratological features. They are evidently developed from the stool shoots of an older tree and of an age that would permit such a tree to have been cut down since the settlement of the region, being 2–3^{dm} in diameter. There were originally five,

one having been cut down and one is dead though still standing. Since they are so close as now to be uniting at the base and have the habit of those springing from a stump, this seems the true explanation of the group. This is important for it suggests if it does not imply the same habit in the tree from which they have sprung. The three trees agree in having the stamens, or perhaps more properly, the filaments of the aments transformed into styles. Numerous flowers have been examined without finding any ordinary stamens. Such may be produced as the aments are borne in profusion. Sometimes the styles or transformed filaments are a little enlarged at the base, but no ovules or traces of them have been found. A minute embryological investigation has not been undertaken. Another teratological feature is the branching or forking of the rachis, or the production of leaves at its end. In this is seen a tendency of the ament to change its function from the reproductive to the vegetative. Since the styles are transformed filaments or substitutes for them, it may be asked, in the case of a monœcious plant at least, whether the male or female element is at the farthest remove from the vegetative. These aments are short lived, lasting about as long as ordinary male aments. The normal pistillate flowers are also regularly produced, and since the trees ripen an abundance of acorns the change in no way seems to interfere with their reproductive power. Cross fertilization becomes a necessity in this case, the trees being functionally diœcious. Since this habit of the trees has been verified three springs in succession, it may be looked upon as fixed. In character they accord best with *Q. coccinea*, but are not typical, being one of the forms which closely approach *Q. velutina*. A detailed description of its peculiarities is subjoined.

Aments producing styles or pistils in place of stamens. They are from 1–3^{cm} long including the peduncle, which is usually short, in some cases 1^{cm} long. Styles four or five, mostly four, flattened, about 2^{mm} long, projecting considerably beyond the rim of the calyx. The base is hairy, dark colored, and when enlarged oblong. They are paler above, slightly curved outward, with the tip usually enlarged like a stigma, but smaller than the stigmas of the normal flower. The enlargement is commonly confined to three as if representing the three styles of the fertile flower. The calyx is hairy, narrowly urceolate, the four or five segments united two-thirds or three-fourths of the way to the top. Its shape is more like that of the pistillate flower than the more open and campanulate calyx of the staminate flower. In

HILL on QUERCUS COCCINEA × PALUSTRIS.



HILL on an ABNORMAL OAK.

some aments the rachis ends in a leafy shoot. One examined had three leaves, one of them small and rudimentary, two being lobed and toothed, the blade 8^{mm} long by 2 or 3^{mm} wide, on petioles 3 or 4^{mm} long (*fig. 1, a*). Another ament was found 15^{mm} long, branched near the top, one branch bearing transformed stamens, the other with a leaf similar to the above but slightly larger.—E. J. HILL, *Chicago.*

EXPLANATION OF PLATES V, VI.

PLATE V. Quercus coccinea × palustris.

FIG. 1. Flowering branch, natural size.

FIG. 2. Pistillate flower. × 6.

FIG. 3. Staminate flower. × 6.

FIG. 4. Leaf, natural size.

FIG. 5. Acorns, natural size.

PLATE VI. Teratological form.

FIG. 1. Flowering branch, natural size.

FIG. 2. Portion of ament. × 6.

FIG. 3. Flower. × 12.

FIG. 4. Leaf, reduced one-half.

CURRENT LITERATURE.

BOOK REVIEWS.

The pruning-book.[1]

THIS book, the latest of the "Gardencraft Series," like all of Professor Bailey's works, deals with the subject in hand from a scientific standpoint, is systematic in arrangement, and so practical in all its suggestions that the average fruit-grower cannot fail to derive much valuable information from a perusal of its pages.

The book is divided into two parts. Part I treats of the "Fundamentals," and Part II the "Incidentals."

In the first part the philosophy and principles of pruning are discussed at length, and in the arguments brought forth it is made very evident to the most casual observer that the author is a firm believer in the theory of evolution as affecting plants, as well as animals. Consequently many of the reasons advanced for certain statements are comparatively new to us, because no American writer has ever taken so advanced a position on this subject as Professor Bailey has done; not so marked perhaps in this as in *The Survival of the Unlike*, which makes a good companion to the present volume.

A very common opinion held by practical horticulturists of the present day is that pruning exhausts the vitality of plants to a greater or less degree, according to the severity of the operation. In discussing this question the author maintains that no injury is done to the plant when the pruning is properly performed, and in support of this statement he presents arguments from three sources, viz., philosophy, plant physiology, and common experience. A tree, he says, is essentially a collection or colony of individual parts. Every branch is endeavoring to do what every other branch does — bear leaves, flowers, and seeds. Every branch competes with every other branch, and there are more rudiments of branches — that is, more buds — than there can be branches upon any tree. The limbs and organs of an animal are not competitors but copartners, each performing some function or office which another does not, and they all obtain at maturity a definite size and shape. But a branch never obtains its full size until it ceases to grow and thereby begins to die. Branches are competing individuals; hence there is a struggle

[1] BAILEY, L. H.: The pruning-book. A monograph of the pruning and training of plants as applied to American conditions. 12mo. pp. xii + 537. New York: The Macmillan Co. $1.50.

for existence among the branches of a tree, and some of them must perish; the destruction of these branches, therefore, must conduce to the betterment of those that remain.

Most fruit-growers advise early and continuous pruning as a means of saving time, and also to direct the energy of the tree which is put forth to produce these superfluous branches into those which are to remain. Professor Bailey believes that annual pruning is desirable, but he is equally convinced that it does not pay, either in cost of pruning or in good to the tree, to cut out all superfluous branches at each pruning. These twigs can often be left till three or four years old with advantage. Pruning in itself cannot be injurious so long as it does not interfere with the nutrition of the plant. Eight reasons are given why pruning should be done.

Part II treats more of the details of everyday practice in starting and shaping the heads of plants; and here the reader is urged to bear in mind the distinction between training or trimming the plant into some desired form, and pruning for definite results in the welfare of the plant and in fruit-bearing.

In discussing the subject of root-pruning the so-called Stringfellow system of stub-root pruning is compared with the ordinary method. Results obtained by the author at the Cornell Experiment Station proved that trees moderately root-pruned were clearly the best. Others, however, have had good results from the Stringfellow method, all of which shows that this method is to be considered a matter of local practice and not a matter of general principle.

The closing chapters of the book treat of training American grapes. The various methods are fully discussed and illustrated, thereby making this one of the most valuable features of the book, especially to the American grape-grower. — J. TROOP.

Fossil botany.

BOTANISTS and geologists both are bound to welcome Professor Seward's work on fossil plants, the first volume of which has recently appeared.[2] This book forms one of the familiar Cambridge "Natural Science Manuals," and is rather more extensive than the others. It is surely safe to say that no general work on paleobotany had yet appeared in English that is satisfactory to both botanists and geologists, and very few that are satisfactory to either. Thus it is a pleasure to read in the preface that this book is intended for both botanists and geologists, and hence has to be adapted to both non-geologists and non-botanists, since it is unfortunately true that neither class as a

[2] SEWARD, A. C.: Fossil plants for students of botany and geology. Vol. I. pp. 450, with illustrations. Cambridge: University Press. 1898.

rule appreciates the standpoint of the other. The first chapter contains a brief historical sketch of paleobotany, in which the author gives special credit to Brongniart and Williamson. Chapter two gives the relation of the subject to botany and geology. Professor Seward tells how paleobotany has been buffeted about by the geologist and the botanist, the one culling out facts relating to the correlation of strata, the other caring only for facts which give hints as to phylogeny and evolution. He pleads for the recognition of paleobotany as a science of and for itself, with its own peculiar problems, viz., the determination of the historical succession of plants in geological time; the delineation of the actual evolution of the plant kingdom, giving light on phylogenetic mysteries; the presentation of the various floral areas of the past, leading up to an explanation of the distribution of plants in the present day; conclusions as to climatic and other conditions in geological time, as revealed by the occurrence of certain peculiar plant types and by anatomical adaptations to environment.

The third chapter gives the leading facts of geological history and is designed for botanical readers.

The next chapter discusses the various methods for the preservation of plants as fossils; structure unmodified, as in fossil soils and forests; carbonization; incrustation, as travertine; casts; petrifactions. The relative rarity of plant fossils is due to their soft structure and land habitats. Chapter five is exceedingly interesting and valuable, as it demonstrates the enormous difficulties and sources of error, such as (1) the danger of depending too much on external resemblances, since many forms from algæ up to seed plants may look alike, even in modern forms, much more in fossils; (2) fragmental preservation (this is much more common than in animal fossils, and also leads to much more error, since a plant often can be identified only in fruit); (3) the decorticated trunks and pith cylinders; (4) resemblance to animals or animal tracks and mineral deposits.

After a chapter on nomenclature, the author takes up the plants by groups. In this first volume he treats only of the thallophytes, bryophytes, and some pteridophytes. Among the algæ there is an abundance of undoubted fossil blue-green algæ, forming deposits of travertine and possibly oolite; Professor Seward thinks that similar forms probably represented the first life of the Algonkian. Because of their siliceous tests there are vast deposits of diatoms, mainly from the Cretaceous on. Of the larger marine algæ those forms are especially preserved which are covered during life by calcareous incrustations, especially the corallines. Many plants of all kinds and many mineral deposits, rill marks, and animal tracks have been referred to the algæ, and especially to the fucoids. Among the fungi there are abundant evidences of fossil bacteria, but the higher forms are rare, though found in the Carboniferous and Tertiary. The liverworts and mosses are poorly preserved and difficult to identify. Of the pteridophytes, the author

considers in this volume only the Equisetales and Sphenophyllales. Both of these groups are abundantly preserved and well known. At the close of the volume is an excellent bibliography.

This work has at least three features to commend it that are by no means common to all books on paleobotany. It is extremely cautious in its statements; many forms commonly described are either classified tentatively or omitted altogether; there are not so many startling allusions to high grade plants in the early ages, but there are more real facts on which to base safe conclusions. Another valuable feature of the book is that important facts have been culled out from a mass of unimportant material, and by no means least in its commendable qualities is that it is actually readable; even the botanical or geological layman may enjoy it, if he cares for such things at all. Everyone who reads the first volume will anxiously await the appearance of the second.—HENRY C. COWLES.

MINOR NOTICES.

DR. L. M. UNDERWOOD read a wise and vigorous paper on the study of botany in high schools before the New York Science Teachers' Association last December. Copies from the *Journal of Pedagogy* for April have been distributed.

DR. W. F. GANONG published in this journal seven years ago (May 1891) a brief account of the raised peat bogs of New Brunswick. During the summers of 1895 and 1896 he was able to give these additional study, and has now published a much more complete and detailed description of the ecological and physical features of these interesting areas.[3]—C. R. B.

TWO BULLETINS of the U. S. Forestry Division have recently been issued.

Bulletin no. 15 is by F. V. Coville, on "Forest growth and sheep grazing in the Cascade mountains of Oregon." It furnishes an account of the methods of sheep grazing on the government reservations in the region named, and their relation to forest preservation both from overgrazing and from fires. Under recent legislation the Interior Department is empowered to make regulations governing grazing on public lands. This report suggests an equitable and apparently feasible system.

Bulletin no. 16 discusses the "Forestry conditions and interests of Wisconsin." It presents the information acquired by Mr. Filibert Roth, a special agent of the department, who made a forest census under the auspices of the state forestry commission and the natural history survey. Botanists will be glad to know that Wisconsin is awakening to an interest in rational forest management. The recommendations of Dr. Fernow, based upon the infor-

[3] Transactions of the Royal Society of Canada II. **2**: 131–163. *figs. 11.* 1897.

mation gathered by Mr. Roth, are as follows: (1) the appointment of a permanent forest commissioner or commission and a fire warden with suitable powers; (2) state control of the manner of exploiting the forest resources; (3) the acquisition of forest lands by the state at their market value, to be paid for in non-taxable scrip bearing 3 per cent. interest, payable after thirty years in yearly payments equaling 10 per cent. of the principal and accumulated interest; and (4) the good management of these lands by the employment of technical skill. To the latter end it is recommended that instruction in forestry be provided at the state university.—C. R. B.

DR. J. C. ARTHUR describes in *Proceedings* of the Indiana Academy of Science for 1897 a simple arrangement for securing uniform water power for use with physiological apparatus. He uses a tank, set in the upper story of the building, and kept filled from the city water supply by an automatic float valve, such as is used for water closet tanks. A small lead pipe, which can be put in place without skilled labor, siphons the water over the top of the tank — he uses a barrel — and is closed by a piece of rubber tubing and a pinch-cock below. A head of fifteen feet is sufficient to run a water motor which will drive a centrifuge. The uniform pressure is useful for many other purposes.—C. R. B.

DR. A. J. GROUT has prepared a list of the mosses of Vermont represented in the collections of Messrs. C. C. Frost, C. G. Blanchard, C. E. and E. Faxon, G. G. Kennedy, Mrs. E. G. Britton, and the author.[4] Dichotomous keys to both genera and species are provided, so that determinations are much facilitated. A number of species, reported but not known to be represented by specimens, are enumerated in a separate list. The arrangement of families and the nomenclature are modernized.—C. R. B.

THE NUMBER of species and varieties, not to mention the forms and subforms, of Sphagnum has grown so great and the synonymy is so intricate and confused that it is almost impossible for even a bryologist who is not a sphagnologist to find his way through the maze. M. Jules Cardot, an able student of this genus, has rendered his fellow bryologists a most acceptable service by publishing a catalogue of all the species and varieties, giving the synonymy, bibliography, and geographical distribution.[5] It is based upon the most recent work, especially upon Warnstorf's comprehensive studies.

[4] GROUT, A. J.—A list of the mosses of Vermont with analytical keys to the genera and species. 8vo. pp. 40. Published by the Botanical Department of the University of Vermont. 15 Mr. 1898.

[5] CARDOT, JULES.— Répertoire sphagnologique: catalogue alphabétique de toutes les espèces et variétés du genre Sphagnum, avec la synonymie, la bibliographie et la distribution géographique, d'après les travaux le plus récents. 8vo. pp. 200. Autun: De Jussieu Père et Fils. 1897.

Though obliged on account of their number to omit the forms and subforms, the catalogue contains 215 species, almost 600 varieties, and about 2000 bibliographical citations. The names are all alphabetically arranged, so that reference is easy. Synonyms appear in their proper place alphabetically and are also grouped chronologically under the species to which they are referred. Such work as this is too little appreciated, but deserves the fullest recognition because it saves others hours of time and does a great deal to facilitate study.

The paper is reprinted (and repaged) from the tenth volume of the *Bulletin de la Société d'Histoire Naturelle d'Autun* (for 1897), the first page of text (p. 3) corresponding to p. 235 of that volume.—C. R. B.

NOTES FOR STUDENTS.

IT IS CURIOUS to find M. Henri Coupin, in experiments to determine the toxic dose of various substances for plants, using *percentage* solutions. If the new knowledge of solutions has taught physiologists anything, it is that percentage solutions of different substances are absolutely incomparable, and to base a comparative research on them now is absurd. The first paper of a promised series is on the toxicity of sodium chloride and sea water.[6] The seedlings of peas and wheat were supported at the surface of the solutions by pins, whose corrosion no doubt adds considerably to the toxicity of the fluids. With such sources of error, the series of experiments does not promise to be valuable.—C. R. B.

MOST INVESTIGATIONS as to the effect of the X-rays seem to be yielding negative results. Schober and Müller find no heliotropic action; Beauregard and Guichard, and Atkinson find that they do not affect the vitality of bacteria; the latter also observed no effect on oscillarias or the sensitive plant. MM. Maldiney and Thouvenin now report[7] that the X-rays have no effect in the formation of chlorophyll. These investigators, however, show that the germination of certain seeds is hastened by exposure for an hour or more to X-rays.

THE LLOYD LIBRARY is coming to be known throughout this country and Europe as one of the most important botanical libraries. Two years ago we asked Mr. C. G. Lloyd to prepare for the GAZETTE a brief account of this library. He acceded to this request, but his absorption in other work and his frequent prolonged absences from this country have interfered with the plan. Now a description of the library has been published by Dr. E. Kremers, editor of the *Pharmaceutical Review*, in that journal (**16**: 85–94.

[6] Revue général de Botanique **10**: 177. May 1898.

[7] Revue général de Botanique **10**: 81. 1898.

1898). To that description we refer our readers. A few of its salient facts we reproduce here.

The founders of the library are John Uri Lloyd and Curtis Gates Lloyd, brothers, who constitute the firm of Lloyd Brothers, extensive manufacturing pharmacists of Cincinnati. The small collection of text-books purchased by the two brothers while serving their apprenticeship in drug stores, constitutes the nucleus of the present handsome library. It has been found advisable to divide it into two departments, one embracing pure botany, in charge of C. G. Lloyd; the other, embracing medical botany, pharmacognosy, pharmacy, and related branches, in charge of J. U. Lloyd, and since 1894 in custody of his assistant, Dr. S. Waldbott. The library is being constantly enlarged by the liberal acquisition of new books and serials. It now comprises approximately 4000 volumes and 1000 pamphlets in the pharmaceutical department, and about 5500 volumes and 3000 pamphlets in the botanical division. There is also in the same building a large herbarium and about 1500 jars of fleshy fungi preserved in alcohol. A building at 224 Court street was purchased in 1891 to house these collections, and though it was then considered ample for some years to come, it had to be enlarged in area and a third story added in 1895 to accommodate the increase. Persons who desire to utilize the exceptional facilities of the library are accorded every possible privilege at Cincinnati, and books are even generously loaned to those at a distance. Professor Flückiger was struck by the remarkable resources of this library when on a visit to this country some years ago, and endeavored to persuade Mr. Lloyd to donate it to some German University. But its founders have determined to donate or bequeath it intact to some educational institution in this country where it can accomplish the most good.—C. R. B.

FOR MORE THAN forty years, notwithstanding close search and careful experimentation, no one was able to add much of importance to the descriptions given by Hofmeister and Mettenius of the gametophytes of Botrychium and Ophioglossum. Hence, when Mr. E. C. Jeffrey published a preliminary statement in the *Annals of Botany* announcing his discovery of more than six hundred prothallia of *Botrychium Virginianum*, botanists awaited the full results of his studies with considerable interest. These have now been published,[8] and, as was expected, prove to be a most valuable contribution to morphology, and by far the most complete investigation of the gametophyte of any of the Ophioglossaceæ that has yet been made. Only one gap in the life history now remains to be filled, viz., that between the chlorophyll-bearing three-celled prothallia obtained from the spores by Professor Campbell, and the tuberous saprophytic form of the mature prothallia.

The prothallia of *Botrychium Virginianum* are oval in shape, destitute of

[8] The gametophyte of *Botrychium Virginianum*. Edward C. Jeffrey. Trans. Canadian Institute —: 265–294. 1896–7.

chlorophyll, and entirely subterranean, ranging in size from 2 to 20^{mm} in length, and from 1.5 to 15^{mm} in breadth. Growth is carried on by means of an apical meristem of probably a single cell situated on the upper anterior side. All the prothallia found were infected with an intracellular endophytic fungus which occupies the lower portion of the gametophyte body, with the exception of two or three outer layers of cells. This fungus Mr. Jeffrey regards as intermediate between a Completoria and a Pythium, since it agrees with the former in its mode of penetration into the host and its possession of large vesicles, and with the latter in the formation of its conidia and the structure of the filamentous part.

The reproductive organs are confined to a median ridge on the upper surface of the prothallium. The antheridia, in mode of origin and development, agree pretty closely with those of other eusporangiate pteridophytes, but the antheridial wall becomes two-layered. The spermatozoids are of the usual filicineous type, large and multiciliate. In the developing spermatozoids no structure was observed comparable to the blepharoplast of Zamia described by Webber, or the "Nebenkern" seen by Belajeff in Filicineæ and Equisetineæ. The archegonium also originates in a superficial cell. It does not differ strikingly from other fern archegonia, but conforms more closely to those of the higher Leptosporangiatæ than to those of Marattia and Ophioglossum, having a protruding neck, small evanescent ventral canal cell, and non-septate binucleate neck canal cell.

Still more interesting is the growth of the embryo. The first or basal wall is transverse, as in all eusporangiate pteridophytes, and median and octant walls follow. But then regularity ceases, and owing to the late appearance of the embryonic organs it was impossible to assign them to definite quadrants of the segmented oospore. The half-grown embryo presents some resemblance to that of Isoetes, since the lower half forms the foot, and the upper half gives rise to stem, cotyledon, and root. Unlike Isoetes, however, but like Equisetum, it has the stem apex differentiated before the first appearance of the cotyledon. The older embryonic organs, except the foot, grow from well-defined apical cells. The gametophyte is remarkably persistent, having been found in one instance attached to a sporophyte eight years old.

Mr. Jeffrey's paper deals also with the stem anatomy of the young sporophyte.

Undoubtedly these results will strengthen the view that the eusporangiate type of pteridophyte is the more primitive. Just which genus is most like the primitive stock it might not be wise at present to conjecture, but it is interesting to note that Botrychium presents points of contact with each of the very divergent lines, Marattiaceæ, Leptosporangiatæ, Isoetaceæ, Equisetineæ, and Lycopodiaceæ.—Wilson R. Smith.

WE CALL ATTENTION to a series of papers which may be overlooked by plant physiologists who fail to keep an eye on the general literature of physiology. These papers record some of the researches of Professor Jacques Loeb and his students in the Hull Physiological Laboratory of the University of Chicago. Several have appeared recently in Pflüger's *Archiv*.[9]

The interest of these papers to botanists lies, of course, in the unity of the facts which they present with those observable in plants, and in the theoretical discussions which must necessarily be applicable to both. Some of these we here summarize.

It is interesting to find that the development of polyps in colonies of *Eudendrium racemosum* is dependent upon light, and that only the more refrangible part of the spectrum is efficient in calling out this reaction; a relation which at once recalls the phenomena of heliotropism, both in plants and animals. Professor Loeb explains this reaction in accordance with Sachs' theory; that under the influence of light certain substances are produced which further the formation of polyps, while in darkness these substances are not produced at all or only in small quantities. On this we remark that these substances are not necessarily the plastic products themselves, but, as Beyerinck suggested, may be substances which act after the fashion of an enzyme to hasten the necessary chemical processes. Indeed, this seems *a priori* more probable.

The peculiar dissolution of the protoplasm of many protozoa on the anodal side when traversed by a constant galvanic current, and the activity of the skin glands of Amblystoma on the anodal side under the same conditions are the reverse of the reaction of the common nerve-muscle preparation, in which, on the closure of the circuit, stimulation begins at the cathode. To explain this discrepancy, Loeb and Budgett seek to establish the theory that the action of a galvanic current on irritable structures is only indirect, the current producing electrolysis. In the nerve-muscle preparation, they would say, there was electrolysis of the internal fluids of these structures. In the exceptional cases above noted, they show that the current produces electrolysis of the surrounding fluid, and that what is called the electrical

[9] LOEB, J.—Ueber den Einfluss des Lichtes auf die Organbildung bei Thieren. Archiv f. die ges. Phys. **63**: 273–292. 1896.

LOEB, J. and BUDGETT, S. P.—Ueber die Ausscheidung electropositiver Ionen an der äusseren Anodenfläche protoplasmatischer Gebilde als Ursache der Abweichungen vom Pflüger'schen Erregungsgesetz. *Ibid.* **65**: 518–534. *pl. 1.* 1897.

LOEB, J.—Zur Theorie der physiologischen Licht- und Schwerkraftwirkungen. *Ibid.* **66**: 439–466. *f. 2.* 1897.

LOEB, J.—Physiologische Untersuchungen über Ionenwirkungen. I Mittheilung. Versuche am Muskel. *Ibid.* **69**: 1–27. 1897.

LOEB, J.—Ueber die physiologische Wirkung elektrischer Wellen. *Ibid.* **69**: 99–114. *f. 9.* 1897.

action of the current is really chemical and molecular (poisoning) action of the electropositive ions set free at the anode, which leads to the formation of alkalies in that region. In support of this they point out that a certain duration of the current is necessary for the production of any reaction, and show that the effect of dilute alkalies is precisely the same as the effect of the current at the anode. The authors think it probable that all galvanic action is indirect in the same sense.

In the paper on the theory of the physiological action of light and gravity, Professor Loeb expresses confidence in the complete analogy between electric and photic stimuli; theorizes on the source of energy for geotropic phenomena; demonstrates clearly (in certain cases at least) the mechanics of stimulation curves; and discusses the so-called "light sense" of eyeless animals. The energy for geotropic curvatures he ascribes to such change of position of substances in the cell as increases or decreases the surface for chemical reactions. This change is conceived as due to the unequal specific gravity of the different substances which become spatially rearranged when the organ is displaced. Such rearrangement leads, directly or indirectly, to the increase of the chemical reaction surfaces of the materials in the cells on the under side of the stem, and their decrease in those on the upper. This theory reminds us strongly, *mutatis mutandis*, of the oldest explanation of geotropism.

As to the mechanics of curvatures, Loeb holds that in all organisms, animal or plant, whether growing, locomotive, or attached, there is the same variable, viz., contractile protoplasm, whose contraction is brought about by stimuli, and that this contraction is the efficient cause of the curvatures. This agrees well with observations on the shortening of the cells on the concave side of plant organs, and the accumulation of osmotically active substances in the cells of that side. Loeb adds a beautiful demonstration from Campanularia, a hydroid polyp.

In the first of a series of papers on the physiological action of ions, Loeb calls attention to the fact that Kahlenberg and True, who were the first to study this general subject, used as a test organism one which did not permit sufficiently accurate discriminations. Loeb has used muscle, and determined the effect of H and HO ions in equivalent solutions upon the increase of the muscle in weight when immersed in a physiological salt solution. In general it was found that the physiological action of dilute inorganic acids and bases was equal when the number of H or HO ions per unit-volume was equal. For organic acids this was not true, on account of the anions and undissociated molecules. The relative poisonousness of ions of the groups Li, Na, K, Rb, Cs, and Be, Mg, Ca, Sr, Ba depends on the rate of migration of the ions and not on the atomic weight of the elements.—C. R. B.

NEWS.

SOME OF THE treasures of the library of the Missouri Botanical Garden are described by Miss Eva M. Reed in the April number of the *St. Louis Public Library Magazine*. A list of the best botanical books for amateurs, beginners, and young people is appended.

DR. B. E. FERNOW, for many years chief of the U. S. Division of Forestry, has been appointed director of the new College of Forestry of Cornell University. The curriculum of the college will be announced this summer. It will include mathematics, civil engineering, botany (especially dendrology), entomology, physics, chemistry, geology, and meteorology. Mr. Gifford Pinchot has been appointed to succeed Dr. Fernow.

PARIS'S *Index Bryologicus* has now progressed as far as *Thuidium* and will be completed in one more, the fifth, part. One comment on the multiplication of forms and subforms in the genus Sphagnum is too good to allow it to remain buried in this reference work. In a footnote to Röll's Systematik the author remarks: "Spezielle Systematik der Torfmoose. Versuch einer Gruppirung der (Nord-Amerikanischen) Torfmoose nach natürlichen Formenreihen, 36 Formenreihen, 373 Varietäten, 325 Formen und zahlreichen Unter- und Nebenformen enthaltend." Röll in *Flora* 1886. Sit brevius dictum: "Tot specimina, quot nomina." O Lindbergii Schimperique manes!

DR. A. MÖLLER of Eberswalde has undertaken the preparation of a memoir of Fritz Müller, the distinguished naturalist of Brazil. He would be greatly obliged for the assistance of friends and any who were brought into scientific relations with Müller. Letters, especially those with scientifically valuable contents, separates of his earlier publications, information as to distinctions conferred upon him and his connection with scientific societies, notices in newspapers and periodicals — in fact all contributions which will facilitate the preparation of a suitable memoir — are solicited. All materials will be carefully used and returned to the owner.

THE DANISH botanist Johan Lange died at his home in Copenhagen on the third day of April, this year, at the age of eighty. Although Professor Lange devoted most of his time to the study and description of the flora of Denmark, he also published several voluminous works upon the flora of Greenland and Spain; besides a number of articles upon systematic botany, with descriptions of new species from various parts of the world. His principal work, however, was a *Manual of the Danish flora*, and the last ten volumes of *Flora Danica*. He was for twenty years director of the botanical garden at Copenhagen, and presided over the Danish botanical society for twenty-seven years; besides being professor of botany at the Agricultural College at Copenhagen. During this long career Professor Lange gained a world-wide reputation as a botanist, and was elected a member of numerous scientific societies. — THEO. HOLM.